Contributions to the Genetics, Taxonomy, and Ecology of Drosophila pseudoobscura and Its Relatives

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Taxonomy, Geographic Distribution, and Ecology of Drosophila pseudoobscura and Its Relatives

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I

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INTRODUCTION

The flies of the genus *Drosophila* occupy the most important place among the organisms which are used as materials for genetic investigations, and it is no exaggeration to say that since the publication in 1911 of Morgan's classic paper the science of genetics has revolved around *Drosophila* work. Certain species of this genus possess a combination of advantages unrivaled in any other known material: rapid development, great fecundity, hardiness, the ease and relatively small cost with which they can be bred the year round in laboratories, and, finally, the giant chromosomes of the larval salivary glands. The fundamental work was done on *Drosophila melanogaster;* this species is still the best material for the study of the induction of mutations, chromosomal aberrations, and similar problems. It is certainly not, however, the only organism amenable to genetic investigation. For certain problems, for example some problems of developmental genetics where *Drosophila's* small size becomes a disadvantage, other forms are preferable. The mechanisms which control heredity are fundamentally the same in all organisms, no matter to what subdivision of the animal or of the plant kingdom they belong; the principles of genetics are perhaps the most universal of all biological principles. The investigator in genetics is, consequently, free to choose and should choose the organism which offers the most advantage for his study, whether it be in the laboratory or in the field.

For studies on the genetics of natural populations, race formation, and species differentiation, two groups of *Drosophila* species have come to the fore, namely, those related to *D. pseudoobscura* on one hand, and those related to *D. virilis* on the other. As laboratory animals and in the clarity of their chromosomes these species are not much inferior to *D. melanogaster,* and from the standpoint of analysis of natural populations they are superior in certain important respects. *D. melanogaster* is at present nearly cosmopolitan and, at least in the temperate zone, is closely associated with man. Its populations are constantly churned up because of unintentional transport by man. It is known to produce hybrids only with *D. simulans,* and these hybrids are sterile. On the other hand, species related to *D. pseudoobscura* and to *D. virilis* (except *D. virilis* itself) are not intimately associated with man, and within each group there are related species which can be crossed and which produce fertile offspring.

Notwithstanding more than three decades of extensive use of *Drosophila* in genetic studies, the biology of its species, and particularly their life cycles in nature and their ecology, are but little known, and, in fact, have been but little investigated. This deficiency of knowledge is of relatively little moment to the geneticist concerned with these insects only in cultures on a laboratory

shelf. But the genetic phenomena occurring in natural populations are so inti-
mately connected with and conditioned by the biology of the organism that
a student of population genetics can ill afford to ignore these connections. The
present paper contains a review of the information available on the biology
of *Drosophila pseudoobscura* and its nearest relatives, which should serve as
a background for the work on the population genetics of these species. Obser-
vations made in nature have demonstrated that *D. pseudoobscura* has a very
complex biology, many features of which had not been even suspected from
many years' acquaintance with the behavior of *Drosophila* flies in the laboratory.

Taxonomy of Drosophila pseudoobscura and Its Relatives

In 1823 Fallén described a species of *Drosophila* from Sweden which he
named *Drosophila obscura* Fallén. The original description is as follows:

Mas & Fem. In truncis arborum, ad Lärketorp Ostrogothiae & Esperöd Scaniae,
rarior. E Westrogothia quoque missa a Nobil. D. Gyllenhal.—Magnitudo praece-
dentis. Caput thorace vix latius: oculis magnis, rotundis, clypeo verticeque obscuris.
Antennae breves nigrae: articulo ultimo subtruncato. Seta longa pectinata. Thorax
opaco-testaceus, obscurus. Abdomen nigricans. Pedes pallidi. Alae parum l. vix
nigredine tinctae.

Sturtevant (1921) called attention to the existence of a species on the Pacific
coast of the United States which he regarded as identical with *D. obscura*
Fallén. In 1929 Lancefield published an important paper in which he showed
that the American representatives of the supposed *D. obscura* are differenti-
ated into two "races or physiological species," which he designated as race A
and race B. The crosses between these "races" produce offspring which con-
sists of fertile daughters and sterile sons. Furthermore, the "races" are dis-
tinguishable by the chromosome configurations in the males: the Y chromo-
some of "race A" is J-shaped and that of "race B" is V-shaped. The external
morphology of the representatives of both "races" was thought to be identical.

Frolova and Astaurov (1929) found that strains of *Drosophila obscura*
Fallén collected in the vicinity of Moscow, Russia, are easily distinguishable
from an American strain by their chromosomal complements, male genitalia,
body color and body size, and behavior in cultures. The crosses between them
failed to produce hybrids. The American form was, therefore, recognized as
a species distinct from the European one, and named *Drosophila pseudoobscura*
Frolova. Although Frolova and Astaurov were unfamiliar with Lancefield's
discovery of the two "races" in the American form, and although the exact
geographic origin of their American strain is unknown, the chromosome
drawings leave no doubt that the name *D. pseudoobscura* Frolova is properly
applicable to Lancefield's "race A."

Systematics of the European representatives of the *obscura* group of species
remain even now in a completely unsatisfactory state. Among the Moscow
strains which Frolova and Astaurov (1929) had at their disposal there were
two groups distinct in their chromosome configurations from each other

and from the American *D. pseudoobscura*. One group had four pairs of V- or J-shaped and one pair of dotlike chromosomes; another group had three pairs of V-shaped, two pairs of rodlike, and one pair of dotlike chromosomes. Which of these chromosome complements belongs to the true *D. obscura* Fallén is unclear. J. E. Collin (*in* Gordon, 1936) described *D. subobscura* Collin from England, differing from *D. obscura* Fallén by larger sex combs in the male, and by a light brownish-gray, completely unstriped thorax in both sexes; it has five pairs of rodlike and one pair of dotlike chromosomes. Buzzati-Traverso (1940) finds in Italy, Germany, and England five species of the *obscura* group, the chromosome complements of which he describes; the names he suggests for them have no standing under the Rules of Nomenclature, since the mimeographed pamphlet containing them is expressly stated not to be a publication. Nothing whatever is known about the occurrence of these or of related forms in Asia, although their presence in at least the northern part of that continent seems very probable on the basis of general zoogeographic considerations.

Lancefield's "race A" and "race B" have been studied in detail. Dobzhansky and Boche (1933) confirmed the sterility of the male "interracial" hybrids, and found two distinct types of Y chromosome in "race A" and two in "race B." Dobzhansky (1935*a*, 1937*c*, 1939) showed that there are at least five types of Y chromosome in A and three types in B, one of these being common to both "races"; it should be noted that strains of A and B which have similar Y chromosomes occur in different geographic regions. The sterility of the male "interracial" hybrids is due to cooperation of at least several, and probably numerous, genes located in all the chromosomes investigated (Dobzhansky, 1936). The viability of the offspring from backcrosses of hybrid females to males of either parental "race" is distinctly lower than that of the pure "races" or of the F_1 hybrids. This lowering of viability was shown to be due to a maternal effect exerted by mixtures of the chromosomes of the two "races" on the cytoplasm of the eggs deposited by the hybrid females, and also to special genes which seem to have no discernible effects on the genetic backgrounds of the pure parental "races" (Dobzhansky, 1935*d*, 1937*a*; Gottschewski, 1940; Mampell, 1941). Thus, although the F_1 females from A×B crosses are themselves fertile, their offspring are reduced in viability to an extent which would probably be fatal under natural conditions. As stated above, the F_1 males are completely sterile.

Comparative study of the giant salivary-gland chromosomes in "races" A and B has disclosed that the gene arrangements in the XR, the second, and especially in the third chromosome are variable from strain to strain within each "race." The XL chromosomes of the "races" differ constantly by a single inversion; the second chromosomes, despite the intraracial variations, also differ by at least a single inversion; the XR chromosomes are usually different, although the so-called "sex ratio" strains of "race B" have the same gene arrangement as the normal strains of "race A"; the third chromosomes may be either similar or different; the fourth and fifth chromosomes are

alike (Tan, 1935; Dobzhansky and Sturtevant, 1938; see also part II in the present publication). Thus, the "races" can always be distinguished by the gene arrangements in their chromosomes. The two "races" present different physiological reaction systems. At 25° C. the development of B takes several hours longer than that of A (Poulson, 1934). At 25° A deposits more eggs than B, at 19° both "races" are about alike in fecundity, and at 14° C. B is distinctly superior to A; at all temperatures the profiles of the egg-laying curves are different in the two "races" (Dobzhansky, 1935c). The longevity of A in the absence of food is greater than that of B (Lilleland, 1938). The two "races" differ slightly in the rate of oxygen consumption during the pupal stage (Dobzhansky and Poulson, 1935). It will be shown below that A occupies warmer and drier habitats than B. ·

For a number of years all attempts to detect differences in external morphology between the "races" proved unavailing. Genitalia of both sexes were found to be identical by Dobzhansky, and this negative finding was confirmed by G. F. Ferris (oral communication), who kindly consented to re-examine the material. Mather and Dobzhansky (1939) found that the number of teeth in the sex combs is slightly greater in A than in B, and that the wings of B are slightly larger than those of A. Finally, Reed, Williams, and Chadwick (1942) demonstrated that the number of wing beats per unit time during flight is greater in A than in B. This physiological difference also proved to be correlated with a structural one. The authors undertook to calculate a special wing index number, obtained by multiplication of wing area expressed in square millimeters by cubed wing length in millimeters. This index in "race A" was found to vary (in different strains) from 45.7 to 62.8, the average being 55.7, and in "race B" from 68.8 to 76.2, the average being 72.6. In conjunction with the differences in the number of teeth in the sex combs and other characters, this index is probably sufficient to discriminate between A and B on purely morphological grounds.

Because these supposed races are in fact species, although but little differentiated in external morphology, we propose the name *Drosophila persimilis* to replace the inconvenient and biologically meaningless designation "race B." The name *Drosophila pseudoobscura* Frolova is accordingly applicable only to the entity previously designated "race A."[1] The description of the new species follows:

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[1] Ginsburg (1940, p. 26) in discussing the race A–race B problem proposes the name *"lancefieldi$_2$,"* which he treats as a subspecific name, without giving either a description or a valid designation or an unequivocal bibliographical reference, as demanded by the Rules of Nomenclature. The name is therefore a *nomen nudum*, and since it is quoted under *D. pseudoobscura* it must be considered an alternative name for *pseudoobscura*. If the name is considered to be correctly proposed, it is obvious from the original wording that it is applied jointly to *D. pseudoobscura* A and B. To make the composite name valid, it must be restricted to one species or the other. We hereby restrict *lancefieldi$_2$* to *Drosophila pseudoobscura* Frolova (1929, Ztschr. f. Zellforsch. u. mikr. Anat., vol. 10, p. 212), of which it becomes a synonym. The unfortunate way in which the name *lancefieldi* was proposed leaves no other course. The situation has been discussed with several experts on nomenclature, all of whom have recommended the procedure followed above.

Drosophila persimilis, species nova

♂, ♀. Arista with 7, less frequently with 8 or 6 branches. Antennae brown, third joint darker. Front dark brown, orbits lighter. Middle orbital bristle one-third to one-half as long as the other two. Second oral less than half of the first. Face dark brown. Carina much broadened below, slightly sulcate. Palpi brown. Cheeks narrow, their greatest width about one-fifth the diameter of the eye. Eyes dark red, with short pile. Acrostichal hairs in 8 rows. No prescutellars. Anterior scutellars convergent. Thorax brownish black, mesonotum with 3 indistinct grayish longitudinal stripes, 1 in the middle and 2 in the dorsocentral rows. Scutellum brownish black, its sides frequently paler. Pleurae brownish black. Sterno index 0.7–0.8. Legs yellowish brown, femora infuscate. Apicals and preapicals on the first and second, only preapicals on the third tibiae. Two sex combs in the male; the proximal one has 5 to 7 and the distal 4 to 6 teeth; the mean for the proximal comb is between 5.5 and 6.2 and for the distal one between 4.7 and 5.1 (in different samples). Abdomen brownish black. Wings clear, veins brown. Costal index 2.8; fourth-vein index 1.9. Wing area 2.6–2.8 sq. mm; Reed's wing index 68–76. Body length 2.3 mm.

Testes in young males bright orange-red, ellipsoidal, becoming darker and more elongated with age. Spermathecae cup-shaped, brown, chitinized. Ventral receptacle short and broad, folded once but not spiralized.

Metaphase chromosome group consists of V-shaped X chromosomes, three pairs of rod-shaped, and one pair of dotlike autosomes; in the male, the Y chromosome is large, V-shaped, equal- or unequal-armed. In the salivary-gland cells the middle part of the short limb of the X chromosome (XL), containing approximately the sections from 7 to 12, and the middle part of the second chromosome, containing approximately the sections from 52 to 56, are inverted (these section numbers refer to the standard maps of these chromosomes published by Dobzhansky and Tan, 1936).

Geographic distribution: from central British Columbia to Santa Barbara County, California, and from the Pacific Ocean to the eastern slope of the Sierra Nevada and Cascade ranges. Type locality: Reedsport, Oregon.

Differs from Drosophila pseudoobscura Frolova in having a lower average number of teeth in the sex combs, a greater wing area, a higher Reed's wing index, the above-described inversions in the XL and second chromosomes, the V-shaped instead of the usually J-shaped Y chromosome, and in several physiological characters.

It is certain that if any kind of structural difference had been known between D. pseudoobscura and D. persimilis, they would have been classed as species from the start. Calling them races, and designating them by the letters A and B instead of by Latin names, was an attempt to appease conservative taxonomists who continue to adhere to the purely morphological concepts of species and race. Such a course is neither scientifically consistent nor practically sound. The species is the stage in the process of evolutionary divergence at which an array of populations once actually interbreeding or capable of interbreeding has become split into two or more reproductively isolated arrays. Species exist in nature regardless of whether we can or cannot distinguish them by their structural characters. There is no doubt that the great majority of animal and

plant species differ structurally, and that they can be conveniently, and in most cases readily, recognized and delimited by their morphology alone. But it does not follow that any and all species are recognizable by their externally visible structures.

The following evidence can be adduced in support of the thesis that *D. pseudoobscura* and *D. persimilis* are distinct species in accordance with the definition given above. Individuals belonging to these species show a clear, though not an absolute, sexual isolation (Boche, *in* Dobzhansky and Koller, 1938). In the laboratory, strains of these species can be intercrossed; interspecific crosses do not go so easily as the intraspecific ones. The F_1 hybrid males are completely sterile. The F_1 females, backcrossed to males of either parental species, deposit numerous eggs; the backcross progenies, however, show a pronounced constitutional weakness. Nevertheless, in the laboratory, it is possible by repeated backcrossing to transfer small blocks of genes of *D. pseudoobscura* onto the genetic background of *D. persimilis,* or vice versa. The question arises whether such gene transfer takes place in nature as well, and if so whether the transfer occurs frequently enough to produce a permanent bridge between the germ plasms of the two natural populations.

The distribution areas of *D. pseudoobscura* and *D. persimilis* are broadly overlapping, and within the zone of overlap representatives of the two species frequently occur side by side. There is, hence, no question of the gene transfer's being precluded merely by geographical isolation. Numerous population samples from localities where the two species occur together have been examined to detect possible individuals which could be identified as interspecific hybrids. No such individuals have been detected. This is negative evidence, to be sure; it is clear that species crosses do not occur frequently, but we cannot exclude the possibility that they take place from time to time. The problem can be approached from another angle: can we detect any evidence that traits normally associated with *D. pseudoobscura* are occasionally present in populations of *D. persimilis,* or vice versa? If hybridization takes place, even though rarely, such "introgression" of one species genotype into the other (Anderson and Hubricht, 1938) might sometimes be observed. Because of the close structural similarity of the two species, we must look to the chromosomes for such evidence. Three possibilities present themselves:

First, a certain type of Y chromosome (type I, Dobzhansky, 1937c) is found in most populations of *D. persimilis* and also in certain populations of *D. pseudoobscura.* Judged superficially, this fact might be taken as evidence of introgression. This chromosome type, however, has never been found in the populations of *D. pseudoobscura* from California, Oregon, and Washington, where it would be expected because of the presence of *D. persimilis,* but only in populations found in southern Arizona, Mexico, and Guatemala, far removed from the range of that species. The type of Y chromosome is similar in appearance in the two species, but it is not impossible that in reality the

chromosomes in question are different. If they are in fact genetically identical, any hybridization must have taken place in the remote past.

Second, the gene arrangement which is normal for the XR chromosome of *D. pseudoobscura* is found in the "sex ratio" strains of *D. persimilis* (Sturtevant and Dobzhansky, 1936*b*). Could the "sex ratio" condition in *D. persimilis* have arisen through introgressive hybridization with *D. pseudoobscura?* Although the available experimental evidence does not permit a final conclusion, the fact is that the transfer of the XR chromosome of *D. pseudoobscura* onto the genetic background of *D. persimilis* causes sterility rather than the "sex ratio" characteristics.

Third, the gene arrangements found in the XL and second chromosomes of *D. pseudoobscura* have never been found in *D. persimilis,* or vice versa. The "Standard" gene arrangement in the third chromosome occurs, however, in both species and in the same geographical region. It will be shown in the following section that this gene arrangement is phylogenetically very old and may have been present in the ancestral species from which both modern ones developed. In the same way, the occurrence of "weak" and "strong" races in both *D. pseudoobscura* and *D. persimilis* (Dobzhansky, 1937*a* and unpublished data) is more likely a survival of the elements from which the sterility mechanism found in the hybrids between these species has been constructed than a result of introgressive hybridization.

To summarize: although we cannot assert that *D. pseudoobscura* never hybridizes in nature with *D. persimilis,* this hybridization is certainly not frequent enough to constitute a channel for a regular gene exchange. These two forms have reached specific distinction. An objection may still be raised against giving them separate names. After all, the systematic nomenclature has been devised primarily for a practical purpose: labeling specimens. The distinctions between *D. pseudoobscura* and *D. persimilis* are admittedly of a kind which not only does not permit a museum worker easily to distinguish pinned specimens, but is difficult even in living individuals, unless breeding experiments or cytological examination are resorted to. This objection fails to take into account that the methods of systematics have, though slowly, changed in the past, and are at present quite different in different groups of organisms. The time is not remote when entomologists described species entirely on the basis of external structures visible in dried specimens with the aid of a hand lens. Only over the protests of conservatives have the characteristics of the genitalia, which frequently demand examination of dissected and cleared internal organs under a microscope, become an accepted criterion of species distinction in many genera and families. Species of some flatworms, nematodes, and annelids are not distinguishable without microtome sections. Bacteriologists would hardly yield to the suggestion that they distinguish species not by culturing them on artificial media, but by observations on the appearance of the organisms in unstained preparations.

It happens that the characteristics of the chromosomes and the breeding behavior furnish the safest method for distinguishing *D. pseudoobscura* and

D. persimilis. We are far from offering the preposterous advice that hence-forward all entomologists should examine the chromosomes of their species before describing them. The methods of systematics in any given group are determined by the level which the knowledge of this group has attained and by the uses to which this knowledge is being put. Species of *Drosophila* are being used as material for studies not only, and even not mainly, by museum systematists. To call *D. pseudoobscura* and *D. persimilis* "races" is confus-ing not only to geneticists, but also to those systematists who are interested, for their own purposes, in the results of genetic work.[1]

The third North American species of the *obscura* group is *D. miranda,* described by Dobzhansky (1935*b*). It differs from *D. pseudoobscura* and from *D. persimilis* in certain details of morphology, in breeding habits, and in the chromosome structure. The genitalia are identical. The body color, and especially that of the legs, is darker. The body size is larger, and specimens caught in nature are usually recognizable by their size, although specimens of *D. miranda* reared from starved larvae may be smaller than those of *D. pseudoobscura* or *D. persimilis* which have developed on abundant food. The proximal sex combs have 6 to 10 (average 8.4) teeth, and the distal ones 5 to 8 (average 5.8) teeth. The development of *D. miranda* takes longer than that of either *D. pseudoobscura* or *D. persimilis,* and the sexual dimor-phism is greater: in the same culture the males frequently begin to hatch only after all the females have hatched. *D. miranda* is sensitive to high tempera-tures (25° C. being sublethal), and somewhat sluggish in its movements.

The metaphase chromosomes of *D. miranda* females are indistinguishable from those of its relatives, but the males have an odd chromosome number (9) instead of the even one (10). This is due to the singular X^1-X^2-Y heterochromosome mechanism in this species (Dobzhansky, 1935*b*; MacKnight, 1939). Examination of the salivary-gland chromosomes reveals that a large number of changes in the gene arrangement have taken place during the evolutionary process which have led to the separation of *D. miranda* from the ancestral *D. pseudoobscura–D. persimilis* stock. A fact of considerable interest is this: in the three chromosomes in which such comparisons are possible, the gene arrangement of *D. miranda* is one inversion step closer to that of *D. pseudoobscura* than to that of *D. persimilis* (Dobzhansky and Tan, 1936).

Males of *D. miranda* show a pronounced aversion to mating with *D. pseudo-obscura* and *D. persimilis* females, and vice versa. The sexual isolation be-

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[1] A suggestion has been made that forms of *Drosophila* which behave as species but are scarcely or not at all distinguishable in conventional museum specimens be designated as subspecies rather than species. This would make confusion worse confounded. The museum systematist would not be benefited thereby, because he is just as interested in determining the subspecies as he is in knowing the species to which his specimens belong. More important still, the usage of the subspecies category has at last reached a certain stability; subspecies are genetically distinct subdivisions of species which replace each other in space. Unless we believe that species exist in nature only if we can distinguish them with the aid of conventional methods, there is no reason to avoid calling a species a species.

tween *D. miranda* and *D. persimilis* is somewhat stronger than that between
D. miranda and *D. pseudoobscura* (Dobzhansky and Koller, 1938). No natural
hybrids have been found. In the laboratory, the crosses of *D. miranda* females
to males either of *D. pseudoobscura* or of *D. persimilis* produce hybrids of both
sexes, whereas the reciprocal crosses produce only· females and a few excep-
tional males (Dobzhansky, 1937*b*). The F₁ hybrid males have rudimentary
testes and are always sterile. The hybrid females deposit numerous eggs which,
with rare exceptions, produce no larvae; this result is due to grave disturbances
in the behavior of the polar bodies and in cleavage (Kaufmann, 1940). Gene
exchange between *D. miranda* and its relatives is completely impossible in
nature.

Drosophila pseudoobscura, *D. persimilis*, *D. miranda*, and their little-known
Old World relatives form a compact *obscura* species group within the sub-
genus *Sophophora* of the genus *Drosophila*. Another equally close-knit group
within the same subgenus, the *affinis* group, has been revised by Sturtevant
and Dobzhansky (1936*a*) and by Sturtevant (1942). It includes six known
representatives: *D. affinis*, *D. algonquin*, *D. azteca*, *D. athabasca*, *D. narra-
gansett*, and the rare *D. seminole*, all of which occur in North and Central
America. The two species groups appear to be ecologically very close, although
their geographic areas tend to be mutually exclusive (see below). Only a
few of the characters which differentiate the *obscura* and the *affinis* groups
need be named here. In the former the acrostichal hairs in front of the dorso-
central bristles are arranged in eight rows, in the latter in six rows; in the
former the males have two sex combs and ellipsoidal testes, in the latter one
well developed and one rudimentary comb and spiral testes; the ventral semi-
nal receptacle in the females of the *obscura* group is shorter than in the
affinis group. Hybrids may be obtained between *D. athabasca* and *D. azteca*
(Sturtevant and Dobzhansky, 1936*a*), between *D. athabasca* and *D. algonquin*,
and between *D. athabasca* and *D. affinis* (Miller, 1939, 1941). These hybrids are
sterile, except the female hybrids from the *D. algonquin* ♀ × *D. athabasca* ♂ cross,
which are slightly fertile. No hybrids at all are obtainable between the repre-
sentatives of the *obscura* and *affinis* species groups. Other species groups of
Sophophora (Sturtevant, 1942) are obviously too remote from *obscura* to be
relevant to the present discussion.

GEOGRAPHIC DISTRIBUTION

Three species of the *obscura* group occur in North America, and five,
possibly more, are found in Europe and, perhaps, in Asia. Virtually noth-
ing is known about the distribution of the Old World species; that of the
American species is relatively well studied (fig. 1).

Drosophila persimilis occurs from Vancouver Island and central British
Columbia to south-central California, and from the Pacific to the eastern
slope of the Sierra Nevada and Cascade ranges. It is also found in the Coso
and Panamint ranges. The northernmost localities in which the species has

been found are Campbell River on Vancouver Island (about 20 miles from the mouth, alder grove along a creek); forest near 150-mile House, British Columbia; and an alder grove near a stream, about 10 miles northeast of
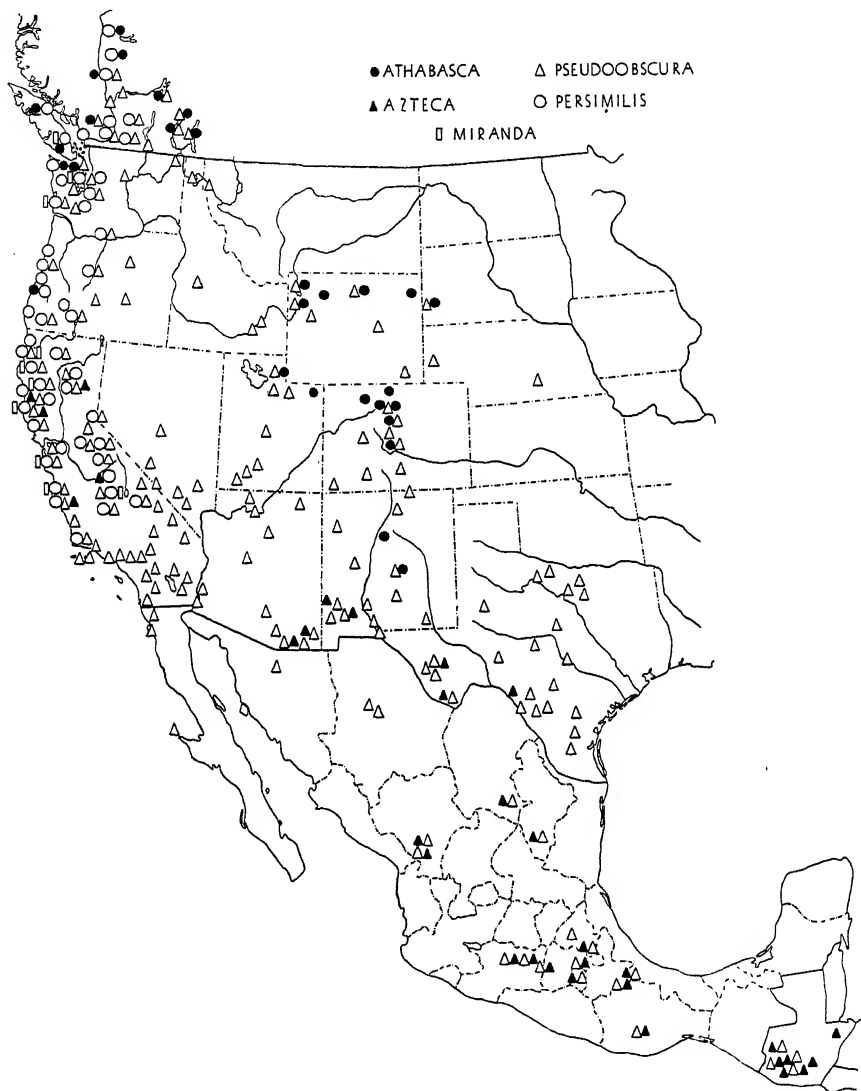
FIG. 1. The known geographic distribution of *Drosophila pseudoobscura*, *D. persimilis*, *D. miranda*, and *D. azteca*, and the southwestern part of the distribution of *D. athabasca*.

Quesnel, British Columbia. Along its northern boundary, *D. persimilis* is replaced by *D. athabasca,* a representative of the *affinis* species group. *D. athabasca* is the commonest species of the genus in Alaska, where it has been found very abundant near Chitina, also at Juneau, Ketchikan, and

Gravina Island; it becomes less common in more southerly regions. Thus, *D. athabasca* is much commoner than *D. persimilis* at Campbell River, 150-mile House, and Quesnel, British Columbia. Slightly farther south, at Cowichan Lake on Vancouver Island, at Cape Flattery and Brinnon, Olympic Peninsula, Washington, and at Pavilion, British Columbia, *D. athabasca* is less common than *D. persimilis*. Farther south, *D. athabasca* has been found only at Reedsport, Oregon. This type of replacement of one form by another along a boundary line which does not coincide with any clear geographic barrier is frequently observed in subspecies of the same species, but it is not common where full species are concerned. It is easy to demonstrate that *D. athabasca* and *D. persimilis* are not subspecies of the same species: no intermediates between them are found in the territory in which they occur together. Although in general adapted to different environmental optima, these two species are ecologically sufficiently similar to tend toward mutual exclusiveness. *D. persimilis* is very common along the Pacific coast from the Olympic Peninsula, Washington, to San Francisco Bay, California. In this region it occurs literally within the sound of the ocean surf, as well as in the mountains. As one proceeds eastward, away from the ocean, into the inner Coast Ranges, the species becomes less frequent. It is very common in the Cascade Range, including the eastern slope thereof (e.g., near the source of the Metolius River, Oregon). In the Sierra Nevada of California, *D. persimilis* is characteristically an inhabitant of the forests at higher elevations. Thus, it has been recorded as common at Manzanita Lake, Mount Lassen National Park; relatively frequent at Deer Creek southwest of Mount Lassen, at Lake Tahoe, at Tuolumne Meadows, Yosemite National Park, and at Mariposa Grove; and again very common in the higher parts of the Sequoia National Park. On the eastern slope of the Sierra Nevada it is common at Mammoth Lakes and in Lone Pine Canyon at the base of Mount Whitney. The southeasternmost known localities are the Coso Range and the southern part of the Panamint Range, in the Death Valley region, California. In the Coast Ranges south of San Francisco Bay the species is relatively uncommon; it has been found on the Monterey Peninsula between Pacific Grove and Carmel, in the pine-oak woodland of the Santa Lucia Mountains northwest of the Tassajara Hot Springs, and, finally, at Nohojui Park, Santa Barbara County. Its southern boundary is, hence, not adequately known. No collecting has been done in the cross ranges which connect the Sierra Nevada and the Coast Ranges at the south (e.g., the Tehachapi Range, Mount Pinos). In southern California the species appears to be wholly absent.

The distribution area of *D. pseudoobscura* (fig. 1) is much wider than that of *D. persimilis,* and the former apparently includes the latter. The only locality from which a rather extensive sample of the population has been analyzed and in which *D. persimilis* but not *D. pseudoobscura* was found is Prairie Creek Redwood Park, near Orick, California. No *D. pseudoobscura* has been found, however, on Vancouver Island, or at Pavilion, 150-mile House, or Quesnel, British Columbia. It is, therefore, probable that *D. pseudoobscura*

does not extend so far north as *D. persimilis,* but more material is necessary to settle this question. The northernmost known localities of *D. pseudoobscura* are Brinnon and Seattle, Washington, and Yale, Princeton, Merritt, Lytton, Kamloops, Lake Shuswap, Arrowhead, Nakusp, and Kaslo, British Columbia. Farther south, *D. pseudoobscura* and *D. persimilis* occur side by side, but an analysis of their distribution makes it strikingly apparent that the former becomes more and more predominant as one moves from regions with a cool and humid oceanic climate to those with a warmer but more continental climate. Thus, *D. pseudoobscura* is generally rare along the coast north of San Francisco Bay, commoner in the valleys between the outer and inner Coast Ranges, still commoner in the lower reaches of the Sierra Nevada, and the only occupant of the territory east of the Sierra Nevada save for the restricted populations in the Coso and Panamint ranges. Altitudinally, *D. pseudoobscura* is more common at lower and *D. persimilis* at higher elevations. Thus, a sample taken in the pine-oak-madroño belt at about 3000 feet on Mount Yollo Bolly (inner Coast Range,ˇ California) consisted predominantly of the former, and a sample in white fir at 6000 feet on the same mountain gave mainly the latter species. In the Sierra Nevada, a sample at Camino, approximately 4000 feet, gave only *D. pseudoobscura,* whereas at Lake Tahoe, 6200 feet, *D. persimilis* is more abundant. In the Sequoia National Park, *D. pseudoobscura* is predominant below 5000 feet, but above 6000 feet both species are equally frequent or *D. persimilis* takes the lead.

Outside the region where *D. pseudoobscura* and *D. persimilis* occur together, the distribution area of the former extends eastward to the Rocky Mountains and Texas and southward to Mexico and Guatemala. In the Rocky Mountains of British Columbia, *D. pseudoobscura* is gradually replaced northward and eastward by *D. athabasca,* the manner of the replacement being the same as described above for *D. persimilis* and *D. athabasca.* A similar replacement occurs in Idaho, Wyoming, Utah, and Colorado, as shown by the following list of localities based on the collecting done by the collaborators of J. T. Patterson and by Th. Dobzhansky. In this list P stands for *D. pseudoobscura* and A for *D. athabasca,* and the figures indicate the number of specimens in the samples collected.

Idaho. Mountains northeast of Boise: P numerous, A none. Pocatello: P 32, A none. Coeur d'Alene: P numerous, A none.

Montana. Bitterroot Mountains near Thompson Falls: P numerous, A none.

Wyoming. Grand Teton National Park: P 5, A 341. Yellowstone National Park: P 6, A 17. Cody: P none, A about a dozen. Big Horn Mountains: P rare, A common. Sundance: P none, A some. Jackson Canyon: P 19, A none. Casper: P 33, A none.

South Dakota. Black Hills: P 33, A 1 (Patterson); P 4, A numerous (Dobzhansky).

Utah. Wasatch Range near Liberty: P 70, A none. Ogden River: P 42, A 9. Cottonwood Canyon southeast of Salt Lake City: P 497, A none. Uinta Mountains near Soapstone: P 17, A none. Uinta Mountains north of Vernal: P none, A 5.

Colorado. Park Range near Columbine Lodge: P none; A 22. Cache la Poudre Canyon near Mishawauka: P none, A about a dozen. Grand Lake: P none, A numerous. Estes Park: P 10, A 12 (Patterson); P 32, A 24 (Dobzhansky). University Camp: P rare, A common. Mount Campbell: P 35, A none. Manitou: P 168, A 1. Colorado Springs, North Cheyenne Park: P 12, A none. Pikes Peak, tree line (about 11,500 feet, the highest collecting locality for the species): P 7, A none. Walsenburg: P 148, A none.

Nebraska. Ponderosa pine forest near Scottsbluff: P some, A none. Gibbon (collected by A. H. Sturtevant): P 1, A none.

New Mexico. Patterson informs us that single females of *D. athabasca* have been collected by G. B. Mainland and R. B. Wagner on July 5 and 7, 1942, at Sulfur Canyon, Sandia Mountains, Bernalillo County, and at Middle Bonita Canyon, Lincoln County. These two localities constitute the southern extremity of the distribution area of the species.

A. P. Blair's collecting in eastern Oklahoma failed to disclose *D. pseudoobscura* there, and the very extensive collecting of Patterson and his colleagues in Texas shows that the eastern boundary of the species in that state is close to the line Wichita Falls—Plano—Fort Worth—Arlington—Florence—Georgetown—Aldrich near Austin—San Antonio—Three Rivers—Alice—Falfurrias. Here it comes in contact with the westernmost extensions of the ranges of two species of the *affinis* group, *D. affinis* and *D. algonquin*. In the forested zone of the western United States *D. pseudoobscura* is by and large the commonest species of the genus, except in the marginal territories discussed above and near man's habitations. In central and southern Mexico and in Guatemala, on the other hand, *D. pseudoobscura* is seldom the predominant species in any climatic or altitudinal belt, and where it does occur it shares the region with *D. azteca,* a member of the *affinis* group (fig. 1). In these countries *D. pseudoobscura* is apparently not found below 5000 feet, and it ranges to at least 10,000 feet (Río Frío, Puebla, Mexico). This range corresponds to the "temperate" and partly to the "cold land" (*tierra templada* and *tierra fría*). Here this species seems to avoid living in the depth of the forest (which it by no means avoids in the United States), and is characteristically found in somewhat drier habitats on the margins of the woods, on slopes covered with sparse tree vegetation, and partly in the brushland. *D. azteca* has the same preferences, but it appears to occur both at lower and at higher elevations than *D. pseudoobscura*. An individual of what was almost certainly *D. azteca* (which, however, was not brought alive to the laboratory) was found on the forested hills above Quirigua, Guatemala, on the edge of a tropical rain forest. *D. azteca* has also been found on the slopes of the volcano Agua at about 8000 feet, and among the pine barrens east of Guatemala City, where *D. pseudoobscura* has not been found.

As would be expected in view of the great extent, both horizontally and vertically, of the distribution range of *D. pseudoobscura,* it occurs in a variety of habitats. In part of the distribution area which lies in the United States it is found wherever trees of any kind grow. Oak and ponderosa pine forests

seem to support the densest populations, but good collections have been made in localities where the only trees were either aspen, or alder, or willow, or piñon pine, or juniper. For some years *D. pseudoobscura* was believed to be attached to forests. Hence its distribution in the southwestern United States, where forests occur on mountain ranges separated by stretches of desert, was regarded as discontinuous. Indeed, as a rule, no *D. pseudoobscura* can be collected during the summer months in desert or semidesert localities in California or Nevada. In March 1936, however, a fair collection was made in the dry course of Gila River, northeast of Yuma, Arizona, where mesquite bushes were the only treelike plants. In May 1938 a few individuals were found among desert vegetation in the higher part of the Mojave Desert (Granite and Ivanpah Mountains), and in the Colorado Desert (Chocolate Mountains, Orocopia Mountains). W. P. Spencer found a single individual at Mesquite Springs, Death Valley. In the spring of 1941, following a winter of abundant precipitation, K. J. Mampell and C. Epling made a series of collections in the Mojave and Colorado deserts (Chuckwalla Mountains, Desert Center, Borego Valley, and Bagdad in California; Yuma, Castle Dome, Tucson, and Sonoita in Arizona). The desert vegetation may, therefore, support populations of *D. pseudoobscura* which may reach considerable densities in the spring season of favorable years. Nevertheless, it would be misleading to describe the distribution of *D. pseudoobscura* in the southwestern United States as perfectly continuous. In the same region the montane forests support larger, denser, and more flourishing populations than the deserts do. Furthermore, in summer, when forest-dwelling populations are most numerous, the desert populations are in eclipse. The desert populations are at their peak when the breeding season in the mountains has barely begun. Freedom of migration from mountain to mountain across the desert stretches is necessarily restricted. The desert colonies may be regarded as exploring parties which have penetrated a less congenial environment.

The distribution area of *D. miranda* is included within that of *D. persimilis,* and hence also that of *D. pseudoobscura* (fig. 1). The species was first described (Dobzhansky, 1935*b*) from Lake Cowichan, Vancouver Island, and mountains near Brinnon, Olympic Peninsula, Washington. An early collection from Seattle contained an individual which might have been *D. miranda,* but subsequent collecting failed to find this species there. Next, *D. miranda* was discovered in Lone Pine Canyon, on the eastern slope of Mount Whitney, California; in this locality it is not rare, and has been collected in three successive years. Astonishingly enough, Lone Pine Canyon is the only locality in the whole Sierra Nevada where the species is known to occur. Rather extensive collecting in the Sequoia National Park, which lies just to the west of Mount Whitney, as well as in other parts of the range has failed to disclose its presence. In 1940 the species was recorded from Willapa Bay, Washington, and from Orick, Coffee Creek, Weott, Mendocino, Big Basin, and the Monterey Peninsula, California. Although it has not been recorded from Oregon, it appears probable that *D. miranda* is distributed more or less continuously

along the Pacific coast from Vancouver Island to the Monterey Peninsula. The Sierra Nevada locality seems, however, to be completely isolated from the main body of the species, a fact which suggests that it was more widely distributed in the past than it is now. Judging by its present distribution, *D. miranda* prefers the humid, cool, and equable oceanic climate even more than does *D. persimilis*.

The distribution areas of the American representatives of the *obscura* group are encircled by those of species belonging to the *affinis* group, except where the former are bounded by the Pacific Ocean (fig. 1). Thus, the area of the *obscura* complex taken as a whole is sharply discontinuous: the three American species are isolated from their European and possible but as yet unknown Asiatic relatives. In the *affinis* group, *D. narragansett, D. seminole, D. affinis,* and *D. algonquin* occur in the eastern United States, the two species last named coming in contact with *D. pseudoobscura* in Texas. *D. athabasca* extends from the Atlantic to the Pacific Ocean; the peculiar replacement of *D. pseudoobscura* and *D. persimilis* at their northern boundaries by *D. athabasca* is described above. The southwestern boundary of *D. athabasca* (fig. 1) is roughly a crescent projecting southward along the Pacific coast (Vancouver Island, Olympic Peninsula, Reedsport in Oregon) and along the Rockies (southward to Colorado and New Mexico), and receding northward in the intermontane region. The species is not known to occur in south-central British Columbia or in eastern Washington.

The distribution of *D. azteca* with relation to that of *D. athabasca* and of the species of the *obscura* group is of interest as a possible source of information on the history of the latter. Be it noted that *D. azteca* is a rather close relative of *D. athabasca,* and is capable of producing sterile hybrids with it. Yet the distribution areas of these two species are separated by those of the *obscura* group, and nowhere, so far as is known, come in contact. In Mexico and Guatemala the distribution of *D. azteca* seems to be continuous, at least in the mountains, but in the United States this species has been found only in several widely separated localities. The southernmost of these (Arizona: Huachuca Mountains, Ramsey Canyon, Cave Creek in Chiricahua Mountains; New Mexico: Glenwood, Silver City; Texas: Davis Mountains, Chisos Mountains, Bracketville; we are greatly obliged to J. T. Patterson for these interesting records obtained by his collaborators) are almost certainly a direct extension of the Mexican part of the distribution area. *D. azteca* has also been found, however, in several scattered localities in California: at Stony Creek and Deer Creek in the Sierra Nevada, and at Pinnacles National Monument, Sebastopol, Hopland, and Guerneville in the Coast Ranges (see fig. 1; the last four localities are based on collections of A. H. Sturtevant). It is virtually certain that further collecting will detect *D. azteca* in other localities in California; nevertheless, there is little doubt that its distribution in California is not continuous. It has been wholly absent from very large samples from Mount San Jacinto and from the Death Valley region, and many smaller but still fairly extensive samples from many localities in California, Nevada,

and northern Arizona. It may be noted that *D. azteca* seems to be not rare in those California localities in which it has been found. The northwestern-most extremity of the distribution area of *D. azteca* (Hopland, California) is not very far removed from the southwesternmost extreme of the area of *D. athabasca* (Reedsport, Oregon), but there remains a gap between them which is not known to be bridged. Similarly, the separation of these two species at the east is also not very wide: *D. azteca* occurs in southern Arizona, southern New Mexico, and southwestern Texas, and *D. athabasca* in the Rocky Mountains as far south as central New Mexico (fig. 1). The combined distributions of *D. azteca* and *D. athabasca* almost encircle those of *D. pseudo-obscura, D. persimilis,* and *D. miranda.*

<div align="center">HABITAT AND FOOD</div>

The standard technique of collecting *Drosophila pseudoobscura* and its relatives in their natural habitats is by attracting them to baited traps. The traps used by us were either half-pint milk bottles or paper drinking cups with a layer of fermented banana on the bottom. In favorable localities and at favorable seasons, several thousand individuals can be taken in a single evening in a territory of about an acre, some traps yielding as many as 200 flies. Under such conditions *Drosophila* populations reach very high densities. Yet if no bait is exposed, these flies are very seldom seen. The favorite collecting method of entomologists, "sweeping" with a collecting net on grass and foliage, catches none, at least in the daytime, when "sweeping" is usually practiced. The normal habitat of the fly is well concealed, and must be learned by a slow process of inference.

By using this method of baited traps in the vicinity of Berlin, N. W. and E. A. Timofeeff-Ressovsky (1940a) found that species of the *obscura* group were continuously distributed over the territory sampled, with scattered nuclei of greater population density. By contrast, *D. melanogaster* and *D. funebris* were found in disjunct islands around compost heaps, fruit and vegetable stores, and the like. We have found that the distribution of *D. pseudoobscura* is like that of its European relatives. Although continuous in distribution, it varies in density seemingly in accord with different microenvironments. Table 1 shows the numbers of individuals in traps exposed at Saunders Meadow, near Idyllwild, California, in June 1942. The traps were arranged in a straight line at 20-meter intervals. Traps A to G stood in a ravine densely shaded by *Pinus ponderosa* and *Libocedrus decurrens,* along which flowed a small stream; traps H to K were on the forest margin, among large oaks (*Quercus Kelloggii*); traps L to O extended onto an open grassy meadow.

Clearly, traps I to K were most productive, and A to E and M to O least frequented. Traps exposed near large oak trees, especially those injured by insects and by woodpeckers, have proved to be consistently productive in different regions. Traps exposed in meadows surrounded by forest are consistently underpopulated, although by no means empty. In these respects, the

data in table 1 may be regarded as characteristic of a much larger body of data, although the relative scarcity of *D. pseudoobscura* in traps A to E in the shaded ravine may have been caused by competition with *D. occidentalis*,

TABLE 1

NUMBERS OF FLIES IN TRAPS EXPOSED IN A SHADED RAVINE (A TO G), ON A FLAT AMONG LARGE OAKS (H TO K), AND ON A MEADOW (L TO O)

Date (1942)	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
June 5	3	1	9	0	7	8	8	15	11	29	80	10	7	4	1
June 6	6	6	7	1	4	5	3	5	2	14	29	5	1	1	0
June 8	7	5	10	4	6	4	10	11	19	33	43	8	3	3	2
June 10	2	7	0	0	3	8	9	4	11	19	52	7	3	2	11
June 11	5	1	1	1	5	2	5	4	3	17	23	8	6	1	2

1	2	3	4	5		
105	78	88	31	82		

6	7	8	9	10	11	12
74	88	53	67	60	114	59

13	14	15	16	17	18	19
99	71	105	93	181	92	66

20	21	22	23	24	25	26
60	66	117	96	97	61	66

27	28	29	30	31	32	33
80	87	101	60	94	38	26

34	35	36	37	38	39	40
68	58	28	22	27	55	38

41	42	43	44	45
79	57	29	21	40

FIG. 2. Numbers of individuals of *Drosophila pseudoobscura* in each of 45 traps arranged checkerboard fashion 20 meters apart on June 18 to 24, 1941, at Keen Camp, California. Note the differences in the intake of the different traps.

which in this particular locality is very abundant and came to the traps by hundreds. Where the latter species is not so prevalent, *D. pseudoobscura* is very common in densely forested habitats. Figure 2 gives the numbers of flies caught on seven successive days (June 18 to 24, 1941) in each of 45 traps

arranged checkerboard fashion at 20-meter intervals near Keen Camp, Mount San Jacinto, California. Day after day some traps gave high yields of flies, while others were less productive. The productive traps nos. 1, 2, 3, 11, 15, 16, 17, 18, 22, 23, 24, 29, and 31 all stood near large pine trees (*P. ponderosa*), on a forest floor covered with a layer of pine needles. Traps 32 to 45 stood in brushland of *Artemisia tridentata* with scattered pines; these traps yielded fewest flies. The remainder of the field was covered with bushes of *Ceanothus cuneatus, Rhamnus californica,* and *Artemisia tridentata,* and scattered pines; the fly yield varied from high (no. 13) to low (no. 4). A similar discontinu-

61 21 *41 89* 48 82	36 7	36 18 *34 122*	78 26 97 115	58 12 *39 74*	9 4	5 1 *6 21* 15 42
11 0	17 4	37 8	25 11	35 10	8 5	10 7
16 6 *7 28*	9 5	15 11 *16 31*	57 20	52 22 *46 127*	11 13	14 16 *33 34*
16 1 7 13	38 9	29 10	20 20 39 44	17 4	12 6	34 9 48 43
5 3 *15 44*	87 9	56 14 *42 62*	27 13	36 10 *18 109*	13 19	7 7 *11 38*
35 3	20 4	40 2	16 4	56 23	37 15	9 3
42 12 *17 58* 52 53	18 2	63 33 *81 96*	38 14 61 73	55 13 *24 68*	35 8	48 10 *39 105* 36 51

FIG. 3. Numbers of individuals of *Drosophila pseudoobscura* in different traps exposed in June 1942 near Idyllwild, California. Further explanation in text.

ous distribution was observed on the field schematically represented in figure 3 (near Idyllwild, California). The traps yielding many flies stood near oak or pine trees; the unproductive traps were mostly in grassy meadows. Again and again it has been observed that traps exposed near trees, especially old and diseased ones, are well attended, and those in brush or meadowland relatively unproductive. The height of the trap above the ground makes little difference, at least in the forest. For example, Alexander Sokoloff placed a series of traps on the trunk of a pine tree from the ground level to about 40 feet; all traps yielded approximately equal numbers of flies. But direct sunlight is decidedly unfavorable.

Since the data point to a connection between the flies and tree vegetation,

a series of "sweepings" with a collecting net on tree trunks was undertaken in July 1942 near Idyllwild, Mount San Jacinto. It yielded several dozen *D. pseudoobscura,* mostly on oaks (*Quercus Kelloggii*), but also on old pines. Therefore, at least some flies take refuge during the daytime in the crevices of oak and pine bark.

The natural food of *D. pseudoobscura* is little known. A. H. Sturtevant found numerous larvae of this species and of *D. persimilis* feeding on the fermenting sap of a wild grapevine (*Vitis californica*) in a forest in Sonoma County, Calfornia. The vine had been injured with an ax, and the sap was dripping on the forest floor. G. Mainland informs us that he has observed adult *D. pseudoobscura* congregating on fruits of a species of *Opuntia* in southern New Mexico. These fruits contained larvae of an undetermined species of *Drosophila.* In the summer of 1941, however, our attention was directed by Pierre Miller to an extraordinary diseased specimen of *Cedrus deodara* in Beverly Hills, California. This tree was suffering severely from a "slime flux," a bacterial infection. Fermenting sap was oozing as froth at various points on the trunk, and the odor of yeast was perceptible several feet away. As it flowed down the bark, this frothy sap became concentrated into a kind of white jelly, resembling library paste. As it dried at the periphery and on the ground or in the crotch of a branch, it took on the consistency and color of moist brown paper. Adult *Drosophila* were abundant around the tree and numerous larvae were to be seen beneath the jelly rather than within it, creeping along the moist crevices of the bark. Their pupae were conspicuous in the drying papery parts. When put into half-pint bottles, these larvae and pupae eventually matured, and from them were recovered numerous adults of the three species most commonly collected in this region: *D. pseudoobscura, D. simulans,* and *D. hydei.*

These observations show that the larvae of *D. pseudoobscura* can feed and mature on the fermenting sap of bleeding trees and in decaying fruit. Whether this is its only, or even its normal, food remains to be decided. At first sight, this seems unlikely. In the arid Southwest flourishing populations can be found in coniferous and mixed forests which in midsummer are extremely dry, and in which neither decaying fruits nor fermenting sap seem to be available. W. P. Spencer has suggested (oral communication) the possibility that in such environments the species may breed in the soil of the forest floor on a diffuse food supply of decomposing plant particles, this breeding taking place only during the seasons when sufficient moisture is available in the soil. The populations found during the dry season are, then, the survivors of the spring brood and will themselves breed in the fall months. This hypothesis has been carefully tested. Although the possibility that some larvae may develop in the soil is not excluded, it seems probable that this is not the norm. In the first place, the flies are known to reproduce and hatch during the course of the dry season (see below). Furthermore, analyses of the fly crops show that the flies have access to supplies of concentrated foods even in the apparently dry forests.

In the summers of 1941 and 1942, at Keen Camp and at Idyllwild, California, flies were attracted to the usual banana traps, but were caught before they had time to ingest the bait. Their crops were dissected at once and the contents examined under a compound microscope. We are greatly indebted to V. P. Sokoloff, of the Citrus Experiment Station, Riverside, who made agar-plate cultures and determined some of the microorganisms thus obtained. Only about 10 per cent of the flies caught had their crops nearly or completely empty and collapsed. Since the contents of the crop pass into the gut within about 24 hours after the ingestion of the food (this point has been determined by experiment), few of the flies had gone foodless for 24 hours or more before being caught. The rest had their crops more or less distended with food. Some flies had their crops filled with practically a pure culture of a single species of microorganism; more frequently the crops contained mixtures of several species. Furthermore, the crop contents varied greatly from fly to fly, even among individuals caught simultaneously at the same collecting station. At least 99 per cent of the nonliquid crop contents were bacteria, yeast cells, and mold spores, named in the order of frequency. The remainder were occasional spores of such fungi as *Diplodia, Cladosporium, Helminthosporium,* rusts or smuts, and amorphous particles of some indeterminate organic matter. A great variety of yeast forms were found, differing in size and shape of the cells and in manner of growth. One very characteristic form suggests *Saccharomyces farinosus,* but was not very common (found in 4 crops among nearly 200 dissected). Some cells resembling *Oïdium* and *Leuconostoc* were also found. Among the bacteria, large and small, single and chain-forming, Gram-positive and Gram-negative cocci were encountered, as well as a variety of rodlike forms of diverse sizes, some Gram-positive and some Gram-negative, either motile or nonmotile. An apparently undescribed species of *Sarcina* gave agar-plate cultures which, in the laboratory, attracted *Drosophila* (V. P. Sokoloff, written communication).

Media of high carbohydrate content seem to be required for the development of many of the microorganisms commonly found in the fly crops. A search for these media in the forest was undertaken, but met with only indifferent success. Moist places were found on the bark of some oaks which had evidently bled earlier in the season; moist decaying areas were found in the crotches of dead branches of others, and under the bark of dying trees and in hollow stumps there were some moist masses of debris produced by wood- and bark-boring insects. Only a single *Drosophila* larva was found in such places, and it was injured in the process of extraction and could not be determined. An examination of the microflora of these materials revealed the presence of forms, both bacteria and yeasts, which appeared to be similar to those found in the fly crops. The possibility that the flies may breed on live trees in the abandoned burrows of wood-boring insects has been suggested, but could not be checked. It is obvious that more observations are necessary to solve the problem regarding the food of *Drosophila pseudoobscura* and *D. persimilis.*

ATTRACTIVE RADIUS OF BANANA TRAPS

Because *Drosophila pseudoobscura* is collected with the aid of banana traps,[1] it is desirable to know from what distance the flies visiting these traps come. A knowledge of this point may help to clarify the problem of the distance traveled by flies in nature in their quest for food. The striking inequalities in the intake of different traps exposed only short distances apart (Dobzhansky, 1939, also table 1 and figs. 2 and 3 above) suggest that the visitors to a given trap are drawn from a limited territory in its immediate vicinity. On the other hand, the fact that traps in a variety of microenvironments are visited to some extent suggests that the attractive radius of a trap may be fairly large, since it is difficult to suppose that the flies are omnipresent. The following experimental procedure was devised by Bruce Wallace and Th. Dobzhansky.

In June 1942, 49 traps were arranged checkerboard fashion (fig. 3), 20 meters apart, in a pine-oak woodland near Idyllwild, California. Approximately 300 meters from this experimental field, a control field with 10 traps located roughly in a circle about 10 meters apart was arranged. On the evenings of June 24 and 26 collections were made from all the traps. The numbers of flies caught are shown in the upper left-hand corners of the squares in figure 3. On June 25 and 28 only the alternate traps were exposed on the experimental field. Consequently, the number of traps was 16 instead of 49, but the distances between them were 40 instead of 20 meters. The slanting numerals in the middle of the squares in figure 3 show the numbers of flies caught on these days. Finally, on June 29 and 30 only 9 traps, 60 meters apart, were exposed on the experimental field; the numbers of flies are shown in the lower right corner of the squares in figure 3. The 10 control traps were, of course, exposed on each of the six evenings. To make the treatment of all the traps equal, the fly collections were made in all the traps simultaneously, by several observers starting and completing the counts by the watch. The average numbers of flies collected per trap are shown in table 2.

The numbers of flies varied greatly on different days, in the experimental as well as in the control traps. This variation was probably due chiefly to weather conditions (fewer flies come on cool days; see below). More important for our present purpose is the fact that when the traps on the experimental field were spaced 20 meters apart, they caught fewer flies than the control traps, whereas traps located 40 or 60 meters apart caught more flies than the controls. This is shown best by the ratios of the fly numbers in the experimental control traps (the right-hand column in table 2). These ratios were significantly higher when the experimental traps were spaced at 40 or 60 meters than when they were located 20 meters apart; the 40- and 60-meter

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[1] Fermenting banana is, of course, not the only substance which attracts the flies. Decaying cantaloupes are at least equal to banana in attracting power. Decaying fruit and vegetables and fermenting liquids of many kinds are commonly visited. *D. pseudoobscura* is only occasionally found on kitchen refuse, and other species, particularly *D. simulans*, *D. melanogaster*, and *D. hydei*, are evidently much superior to it in these environments.

spacings did not differ significantly from each other. It follows that traps 20 meters apart interfere with each other, but those at 40 or 60 meters show no such interference. Since the control field was in a territory more favorable for the flies (denser trees) than the experimental field, the fact that the control traps, though only about 10 meters apart, had more flies than the experimental traps does not contradict the above conclusion.

The objection may be raised that comparing the average numbers of flies in all the traps on the experimental field is unfair. Indeed, different traps on the experimental field of 49 were not equally well attended (see fig. 3). To cope with this objection, the data for June 24 and 26 were recalculated taking into account only those traps which stood in the positions which were subsequently occupied by the traps spaced at 40 or at 60 meters. The average numbers of flies in the 16 traps corresponding to those used on June 25 and 28 are: for June 24, 35.56 ± 5.44; for June 26, 13.06 ± 1.97. The average numbers

TABLE 2

NUMBERS OF FLIES PER TRAP ON THE EXPERIMENTAL AND THE CONTROL FIELDS

Date (1942)	Number of traps	Distance between traps (m.)	Flies per trap		Ratio Exper. : control
			Experimental	Control	
June 24	49	20	30.8 ± 2.8	39.1 ± 4.5	0.79 ± 0.12
June 26	49	20	10.4 ± 1.1	14.1 ± 0.7	0.73 ± 0.08
June 25	16	40	20.3 ± 4.8	22.5 ± 2.4	1.30 ± 0.25
June 28	16	40	69.1 ± 8.8	40.3 ± 5.0	1.72 ± 0.31
June 29	9	60	44.8 ± 8.0	35.7 ± 2.7	1.25 ± 0.24
June 30	9	60	57.3 ± 9.8	43.6 ± 4.6	1.32 ± 0.26

of flies in the 9 traps corresponding to those used on June 29 and 30 are: for June 24, 38.00 ± 7.60; for June 26, 12.67 ± 2.88. The ratios experimental: control are, therefore, 0.91 and 0.97 for June 24, and 0.93 and 0.90 for June 26. Comparing these ratios with those for traps spaced at 40 and at 60 meters (table 2), we find that the ratios for traps at 20 meters are smaller than unity, and for traps at 40 and 60 meters greater.

The most reasonable view is that the probability of a fly's coming to a trap (or to a natural food source) is a function of the distance between them. Most of the flies in the immediate neighborhood of a trap will be attracted to it, and fewer and fewer of the flies at greater distances will come. The absolute attractiveness of a trap will, of course, depend on the nature and quantity of the bait, on the species and physiological condition of the flies, on weather, and on the presence or absence of other sources of attraction in the environment. Therefore, the above data are valid only for *D. pseudoobscura* and only for midsummer conditions on Mount San Jacinto. Under these conditions, the effective attractive radius of a banana trap for *D. pseudoobscura* is hardly more than 30 meters.

⁻Diurnal Periodicity

Under laboratory conditions, species of *Drosophila* seem to be more or less equally active whenever observed. Geneticists who may have worked for many years with them in laboratories are therefore often unaware of the fact that in nature these insects display striking differences in behavior at different times of the day. As early as 1933, when one of the writers first attempted to collect *D. pseudoobscura* and *D. persimilis* in the mountains of California, it was found that by far the most effective time to expose the traps was shortly before sunset or shortly after sunrise. In summer, particularly, it was found that the arrival and disappearance of the flies both night and morning was frequently quite abrupt. N. W. and E. A. Timofeeff-Ressovsky (1940a) have also reported that near Berlin, *D. melanogaster*, *D. funebris*, and species of the *obscura* group are most active during the morning and evening, and scarcely appear at midday and during the night. Our own observations have established a similar behavior for *D. simulans* and for members of the *hydei* group.

A diurnal cycle typical for *D. pseudoobscura* on a warm, cloudless day of early summer on Mount San Jacinto is represented in the upper part of figure 4. The data are based on the output of 10 traps exposed in an open yellow pine forest at Keen Camp, elevation 4300 feet. No flies came between sunrise and 7 A.M.; the temperature during that time rose from 42 to 54° F. A temperature of about 50° F. (10° C.) is apparently limiting for *D. pseudoobscura:* below that, no flies appear. Between 7 and 10 A.M. flies were coming, the maximum abundance being observed around 8 A.M. None came between 10 A.M. and 5 P.M. Another sharp maximum occurred at about 6:30 P.M. Darkness fell shortly after 7 P.M., and the flies left the traps very abruptly: none were left by 7:30 P.M. Another cycle, observed on August 17, 1942, at Bluff Lake, San Bernardino Mountains, California, elevation between 7300 and 7400 feet, is shown in the lower part of figure 4. In this case, 13 traps were exposed in *Pinus contorta–Abies concolor* forest; the amplitude of temperature change was less than on the day discussed above; sunshine alternated with cloudiness. Some flies were present from sunrise on; the morning maximum came around 8 A.M.; from 10 A.M. to 4 P.M. the flies were rare, but at no time were the traps completely deserted; another, and very sharp, maximum was observed at 5:45 P.M.; flies were still abundant at the time of the apparent sunset, at 6:15 P.M.; very few remained at darkness, 6:45 P.M., and none were present at 7:05 P.M. The two cycles shown in figure 4 are astonishingly similar, despite the differences in elevation of the collecting localities, temperature, humidity, and cloudiness. The following differences between the cycles may, however, be noted: (*a*) the flies at Keen Camp appeared later in the morning, probably on account of the lower temperature; (*b*) some flies at Bluff Lake were active at midday; we hope to show below that this is probably ascribable to the cloudiness.

Any attempt to analyze the causation of the diurnal cycles is confronted with

a difficulty inherent in the observational, as contrasted with the experimental, method. Obviously, several variables are changing in the fly environment during the day: light, temperature, humidity, wind, cloudiness, etc. The changes in these variables are neither independent nor subject to our will. The only recourse is to compare the behavior of the flies on different days, at different seasons and places. This we have attempted to do, and the following data
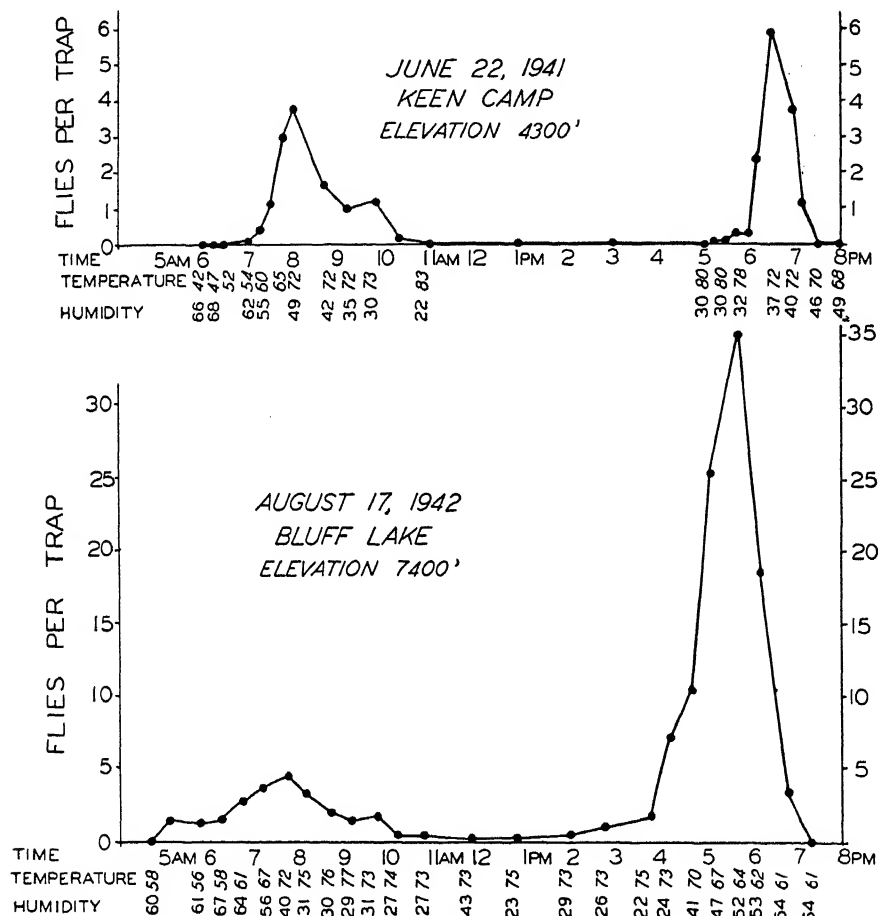
FIG. 4. The diurnal periodicity in the activity of *Drosophila pseudoobscura*

are samples of the material collected. For several years we entertained the hypothesis that temperature and humidity are the primary factors which evoke the activity of the flies during the morning and evening hours; at present we are inclined to believe that light intensity is the primary factor, temperature and humidity being less important.

After analysis of all the data available, the following facts of behavior seem to be established. The invariable rule to which no exceptions have so far

been found is that no flies are active during the hours of darkness, from dusk to dawn. By "activity" we mean in this discussion the flight in search of food which leads the flies to enter traps. Flies have been trapped through a range of relative humidity from 11 per cent to nearly 100 per cent. Although most have been trapped within the range from 30 to 50 per cent, it seems probable that this is merely a reflection of the greater prevalence of days with this range in the parts of southern California where the major part of the work was done. If the temperatures at which collections have been made are held constant for intervals of 5° and the numbers of flies are plotted for different percentages of relative humidity, or if the relative humidity is held constant for intervals of 10 per cent and the numbers of flies are plotted for different degrees of temperature, no preference appears for any combinations of temperature and humidity, whether all stations are included, both morning and evening maxima or either alone, or whether stations are treated separately. Flies have been trapped through a range of temperature from 47.5 to 90° F. If numbers be considered, however, it appears that more have been trapped between 60 and 80°; yet here again, this result seems only to reflect the number of days with these temperatures when recordings were made. If the diurnal maxima of abundance alone are considered, the total range of humidity at which they were recorded is 23 to 71 per cent, and the total range of temperature 55 to 87°. The latter, recorded at Andreas Canyon, is close to the highest temperature at which any flies have been collected, the former not much above the lowest. Only a single fly was caught below 50° F.

At a given collecting station, the numbers of flies encountered on successive days may vary greatly, but, unless clouds or rain intervene, the times of the appearance and disappearance of the flies change but slowly. Figure 5 shows the numbers of flies that came to traps on the afternoons of June 24 to 30, 1942, at Idyllwild (fig. 5 and table 2 describe different aspects of the same experiment). June 26 was cool; the temperature changed from 66° F. at 5:25 P.M. to 56° at 7:05, and the relative humidity from 49 to 69 per cent; the average number of flies per trap was 10.9. June 24 was warmer and drier (73° and 31 per cent at 5:15 P.M., 58° and 50 per cent at 7:15 P.M.); the average number of flies per trap was 32.2. June 28 was still warmer, but less dry (80° and 30 per cent at 5:00 P.M., 61° and 64 per cent at 7:05 P.M.); the average number of flies rose to 58.0. June 30 was the warmest day (81° and 26 per cent at 5:15 P.M., 63° and 54 per cent at 7:05 P.M.); the average number of flies fell to 49.6. Despite these variations, the flies appeared in appreciable numbers at about 5:30 P.M., reached maximum abundance between 6 and 6:30, and disappeared shortly after 7 P.M. on each of these four days (fig. 5).

The independence of the time of appearance, of maximum abundance, and of disappearance of the flies as regards temperature, and the dependence of the number of flies coming to traps on temperature, and possibly on humidity, was observed repeatedly whenever collections were made at the same station on a series of successive cloudless days. Flies come to traps at their customary time, unless the temperature falls to or below 50° F. The possibility that

there may exist also an upper limit of temperature tolerance will be discussed below. Rain and cloudiness change the situation completely. This was observed for the first time in July 1935 in Cimarron Canyon, New Mexico. After a brisk thunderstorm, *D. pseudoobscura* came abundantly from noon until 2 P.M., disappeared thereafter, and returned shortly before sunset. *D. persimilis* and *D. pseudoobscura* have repeatedly been trapped during the day on the coast of northern California, where fog or cloudiness is the rule in summer. From July 23 to August 8, 1941, flies were collected every after-
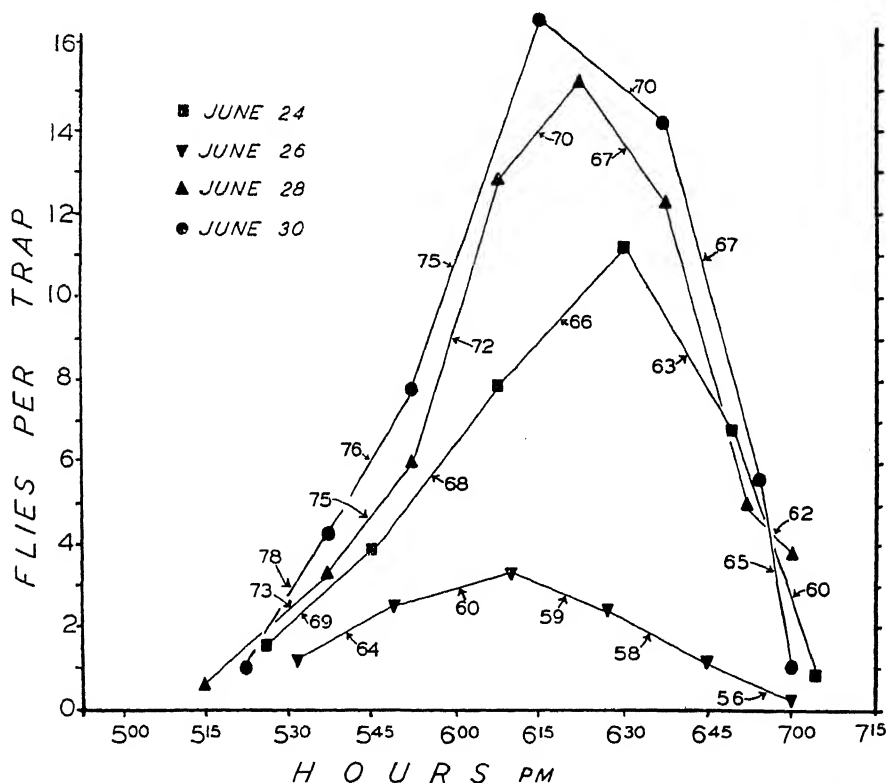
FIG. 5. Numbers of flies attracted to traps on days with different temperatures

noon on the same experimental field at Keen Camp, California. Most of these days were cloudless, and the flies appeared regularly at about 5:00 to 5:30 P.M., reached maximum abundance between 6:10 and 6:45, and disappeared after dark between 7:10 and 7:20 P.M. July 25 was, however, cloudy, and the maximum abundance of the flies was observed at 5:30 P.M. Rain fell on August 7; the flies were about equally abundant from 3:45 (when the experiment started) to 6:10 P.M., and disappeared at 7:05 P.M. Following a long drought, the day of August 9, 1942, was cloudy at Idyllwild. A mist fell around 5:20 A.M., and again at noon, and it rained from 4 P.M. on. On this day *D. pseudoobscura* was abundant from 5 to 9 A.M., rare but still present from 9 A.M. till noon,

and again abundant from noon till 4 P.M. On the clear day of August 12, the flies were abundant from 4:45 to 8 A.M., absent from then till 5 P.M., and present again till about 7 P.M., on the same part of the experimental field on which such different behavior had been observed only three days previously (table 3).

Since cloudiness and rain increase the humidity, usually lower the temperature, and cause the flies to come to traps at any time during the daylight hours, it seemed plausible to ascribe to these factors the evocation of the activity of the flies. As pointed out above, other data are inconsistent with this hypothesis. Since cloudiness has also the effect of diminishing the
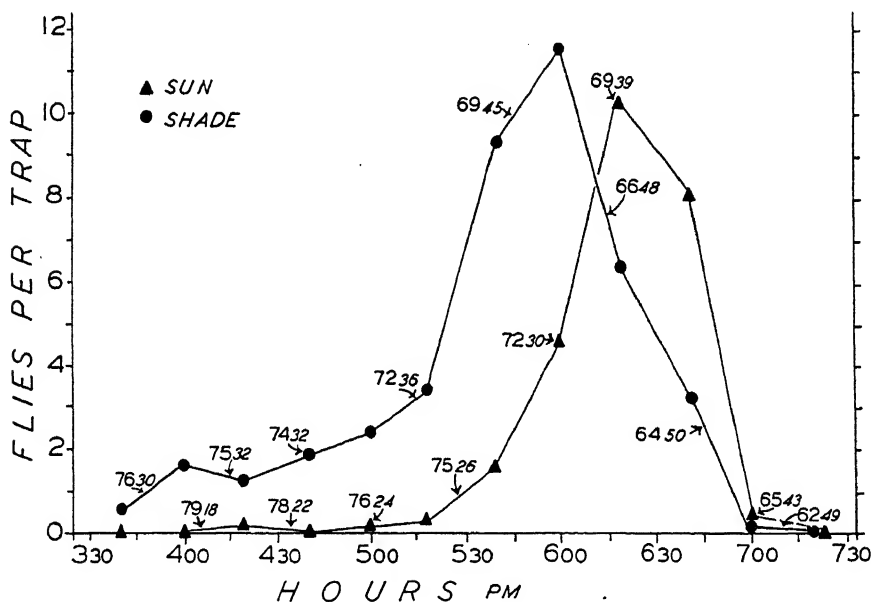
Fig. 6. Numbers of flies which came to traps exposed in a shaded ravine and on sunlit slopes near Idyllwild, California, on July 30, 1942. Larger numerals, temperature in °F.; smaller (slanting) numerals, relative humidity in per cent.

intensity of sunlight, the facts so far presented do not necessarily contradict the view that light intensity is the primary factor determining *Drosophila's* activity. To test this view, the following observations were made. On the afternoon of July 30 a series of 15 traps was exposed in a ravine well shaded by a dense growth of ponderosa pine and *Libocedrus decurrens* at Saunders Meadow, Mount San Jacinto. Another series of 15 traps was exposed simultaneously on the sunlit slopes of the same ravine in a sparse stand of *Pinus Coulteri, P. ponderosa,* and *Quercus chrysolepis.* Although the second series of traps was protected from direct sunlight by the shadows of the tree trunks, the light intensity in their surroundings was obviously greater than in the shaded ravine. Temperature and humidity readings were made both in the ravine and on the slopes. The results are presented in figure 6. The observa-

tions were repeated in the same setting on August 12 during the whole day; this time, however, only 10 traps were exposed in each series, and temperature and humidity readings were taken only in the ravine; the results are presented in table 3. Another repetition fell on the rainy day of August 9, with the results given above. The data in figure 6 and table 3 show concordantly that in a well shaded area *D. pseudoobscura* remains active at all daylight hours even on clear days, whereas no flies come to traps in more open areas except in the morning and the evening. To be sure, the morning and evening maxima are observed in the shaded area as well, but here they are not so sharp as they are in the open. It may be noted that the temperature in the shaded area

TABLE 3

NUMBERS OF FLIES PER TRAP OBSERVED AT DIFFERENT TIMES OF THE DAY ON AUGUST 12, 1942, IN A SHADED RAVINE AND ON SUNLIT SLOPES

| Time (A.M.) | Temp. (°F.) | Humidity (%) | Flies | | Time (P.M.) | Temp. (°F.) | Humidity (%) | Flies | |
			Shade	Sun				Shade	Sun
4:45	58	77	0	1.3	12:10	75	40	0.3	0
5:05	57	82	1.3	12.3	1:05	74	40	0.1	0
5:30	57	75	1.9	4.8	2:00	74	36	0	0
6:00	57	75	1.4	2.4	3:10	74	40	0.2	0
6:30	58	70	1.1	2.6	4:00	73	44	0.3	0
7:05	59	72	0.2	1.1	5:15	71	60	2.9	0.3
8:05	67	70	2.4	1.3	5:45	67	62	4.0	3.8
9:00	70	60	1.5	0	6:15	68	62	4.0	3.8
10:00	75	44	0.1	0	6:45	63	71	0.7	2.1
11:00	74	40	0.1	0	7:30	62	73	0	0

was 3 to 4° F. lower and the relative humidity 10 to 15 per cent higher than in the open area. Figure 5 and other data show, however, that even greater temperature and humidity fluctuations affect only the abundance, not the times of appearance and disappearance of the flies.

Another way to test the relative effects of light and weather on the daily periodicity is to observe the times at which the flies are active in the same locality in different seasons of the year. Still another way is to compare the behavior of the flies at the same season, and preferably on the same day, in localities at different elevations and hence with different temperature and humidity regimes. Obviously, only cloudless or nearly cloudless days are suitable for such comparative observations. Andreas Canyon is a locality lying at the foot of Mount San Jacinto, elevation about 800 feet. Table 4 shows the numbers of flies coming to traps at different hours of the day in that locality; temperature records (Fahrenheit) are also shown in table 4. The flies are common at Andreas in winter and spring, very scarce in late summer. January 11, 1942, was cloudy; flies came to traps from morning till sundown, without a definite maximum. On March 13 a strong wind arose in the afternoon and no flies appeared. Other days recorded in table 4 were clear. In

TABLE 4

Numbers of flies per trap (f) and temperature (t) in degrees Fahrenheit in Andreas Canyon, California

Time	Sept. 9, 1941 t	f	Oct. 3, 1941 t	f	Nov. 8, 1941 t	f	Dec. 7, 1941 t	f	Jan. 11, 1942 t	f	Feb. 3, 1942 t	f	Mar. 13, 1942 t	f	Apr. 3, 1942 t	f	May 2, 1942 t	f	June 12, 1942 t	f
5:00 A.M.	66	0	58	0															67	<1
5:30	64	0.7	51	0	55	0							50	0					65	<1
6:00	64	3.2	55	0.1	54	0							47	0	66	0				
6:30	66	1.5	59	0.1	55	0.1							50	0	65	1.9			69	0
7:00	67	1.1	59	0	56	0	44	0			51	0	56	0	66	2.1				
7:30	68	1.2	65	0.2	58	0.1	52	0					59	2.8	72	1.2				
8:00	72	0.7	66	0.2	61	0.6	54	0			55	0.4	58	3.7	73	0.2				
8:30	77	0	69	0	66	0.4	61	0.1	57	0			60	2.6	76	0.3				
9:00	80	0			68	0.1	63	0.4	64	0	62	0.8	61	1.1	79	0				
9:30					74	0.1	69	0.2	68	0.6			61	0.5						
10:00					71	0.2	70	0.1	70	0.4	64	0.8	60	0.1	81	0.4				
10:30					75	0.1	71	0.1	72	0.6			65	0.3						
11:00					78	0	72	0.2	70	0.2	68	0.3	68	0.2	81	0				
Noon					79	0	73	0	75	0.3	68	0	77	0.1						
1:00 P.M.					80	0.1	75	0.2	73	0	70	0.2	70	0						
2:00					75	0	73	0.1	75	0.5	74	0			83	0.2				
2:30					73	0.1	70	0.4	73	0.3					84	0				
3:00			74	0.1	72	0.5	68	0.7	70	0.6	74	0.2	64	0	82	0.5			91	0
3:30			76	0.1	67	1.3	62	1.0	67	0.8	71	0.9			82	0.8			94	0
4:00	89	0.4	68	0.9	66	1.3	64	0.7	64	0.2	65	3.0	59	0	81	2.2	78	0.6	88	0
4:30	87	1.0	66	0.6	70	0.9	57	0	60	0.2	65	2.9			78	12.2	77	2.0	87	<1
5:00	88	3.5	64	0.2	66	0.1			58	0	63	1.7	61	0			75	6.0	84	<1
5:30	85	1.0	64	0	64	0					58	0.4					72	6.5	81	<1
6:00	87	2.2			62	0											68	3.5	78	<1
6:30					62	0											67	1.5		
7:00																	67	0.1	77	<1

September, October, May, and June flies were coming to traps only in the mornings and the evenings. In May the evening maximum of abundance of flies was observed around 5:30 P.M., the temperature at that time being 72°; in September the evening maximum came around 5:00 P.M., temperature 88°; in October the maximum was at about 4:00 P.M., temperature 68°. Clearly, the evening maxima come at very different temperatures, and, we may add, at different humidities. With the advent of short winter days, in November and December, the morning and evening maxima approached each other to such an extent that only a short period in the middle of the day showed no activity on the part of the flies. In winter, however, the flies appear late and disappear early. On December 7 the first fly came at 8:30 A.M., which is later than the end of the morning activity in September, and the last fly was observed at 4:30 P.M., which is the time when flies just begin to come to traps in September, May, and June. The temperature during the evening maximum of abundance of flies in November was 66–67° F., and in December 62°. The evening maxima come, therefore, at temperatures from 62 to 88°. Morning maxima are generally less definite, but the data in table 4 record them at temperatures from 58 to 66° F. Meteorological data for Riverside, California (about 40 miles from Mount San Jacinto) show that the morning twilight in June begins at about 3 A.M., sunrise is at 4:45 A.M., sunset at 7:20 P.M., and the end of the evening twilight at 9 P.M.; in December the morning twilight comes at 5:40 A.M., sunrise at 7:10 A.M., sunset at 4:45 P.M., and the end of the evening twilight at 6:20 P.M. Even more interesting and pertinent are the data for light intensity at different hours of the day and at different seasons. The light intensity has been measured in terms of gram-calories per square centimeter of horizontal surface. The intensities between 10 and 30 gram-calories are observed between 6:40 and 8 A.M. and between 5:15 and 6:40 P.M. on June 21, and between 8:50 and 11:15 A.M. and between 1:30 and 4:10 P.M. on December 23. We are indebted to the University of California, Citrus Experiment Station, Riverside for these meteorological data. The hypothesis that the activity of the flies is determined by the light intensity seems to be on the whole consistent with the known facts.

Comparison of the times of appearance, maximum abundance, and disappearance of the flies in localities at different elevations is made difficult by the seasonal variations in their abundance. At low elevations the flies are scarce in summer, whereas at high ones they are not to be found in winter. We have tried to assemble data for Andreas Canyon (elevation 800 feet), Piñon Flat (4000 feet), and Keen Camp (4300 feet), all within 10 to 15 miles of one another on Mount San Jacinto. Occasional observations have been made also in divers other localities. The tabulation on page 33 summarizes some of the data on the hours of the afternoon at which the maximum of abundance of flies is observed, and on temperatures (Fahrenheit) prevailing at these hours.

The maxima as well as the arrival and disappearance of the flies tend to come at the same time, despite differences in elevation, temperature, humidity, and environment generally at the different stations. At Piñon Flat, however,

the maximum tends to occur a little later than at Andreas Canyon and Keen Camp. This is not clearly shown in the above data, but it has been observed repeatedly. This delay is probably significant, because this station is but little shaded from the setting sun; Andreas Canyon has a high mountain lying to the west of it, and it passes into shade long before sunset; Keen Camp is forested and is also shielded on the west by a mountain range. Whether these facts are sufficient to explain the behavior of the flies at Piñon Flat is not quite clear, but in any case the data as a whole are consistent with the hypothesis that the activity of the flies is determined by light rather than by temperature or humidity.

In the summers of 1941 and 1942 flies marked with a mutant gene or with a spot of paint on the thorax were released at Keen Camp, Piñon Flat, and Idyllwild. (These experiments are described in the following section.) These

HOURS OF THE AFTERNOON AND TEMPERATURES (F.) AT WHICH MAXIMUM ABUNDANCE OF THE FLIES HAS BEEN OBSERVED

Dates	Andreas		Piñon		Keen	
	Time (P.M.)	Temp. (°F.)	Time (P.M.)	Temp. (°F.)	Time (P.M.)	Temp. (°F.)
June 15–17, 1941	....		7:00	72	6:30	70
Sept. 9, 1941	5:00	78	6:00	74	6:00	76
Oct. 3, 1941	4:00	68	5:30	62	4:00	63
Nov. 8, 1941	3:30–4:00	67	4:00	62	3:30–4:00	67
Dec. 6–7, 1941	4:00	62	4:00	55		
Jan. 10–11, 1942	3:30	67	3:30	62		
Apr. 2–3, 1942	5:00	78	5:30	68		
May 2–3, 1942	5:30	72	6:00	66	5:30	63

flies, and their ancestors for several generations, were bred in regular culture bottles in the laboratory. For several consecutive evenings after the liberation of the marked flies, traps were exposed in the neighborhood of the point of release, and the numbers of the marked and wild flies which came to these traps were recorded. These experiments have revealed an astonishing fact: at least at Keen Camp and at Idyllwild, the laboratory-grown flies fell almost immediately into the diurnal cycle characteristic of the wild flies in the same locality. Sometimes for a day or two after the release the marked flies began to arrive in the traps about half an hour before the wild flies did, but on the following days there' was no observable difference between the behavior of the marked and the wild flies. Similar experiments conducted at Piñon Flat in July 1942 suggested that in the hot and arid midsummer climate of that locality the laboratory-grown flies did not adjust themselves quite so success-fully as they did in the milder environments of Keen Camp and Idyllwild. At any rate, only a small fraction of the liberated marked flies were recap-tured, and those which came to traps did so mostly before the wild flies ap-

peared. As indicated above, there is some reason to suspect that the diurnal cycle of the flies at Piñon Flat is somewhat different from that in other parts of Mount San Jacinto. Only experiments can determine to what extent the diurnal periodicity of the flies is inborn and to what extent it is induced by the environment during the fly's development. It is also possible that there may exist geographic races or ecotypes which have somewhat different periodicities; this possibility must be left open.

This hypothesis, that light is the principal causal factor which determines the diurnal periodicity of the flies, explains the data better than any other which we have been able to contrive. Aside from the indications of a peculiar behavior of flies at Piñon Flat (see above), there is only one fact which seems inconsistent with this hypothesis. This is the fact that more time elapses between sunrise and the morning maximum of abundance of the flies than between the afternoon maximum of abundance and sunset (fig. 4, tables 3, 4). The light intensity, of course, increases from morning to noon and decreases from noon to sunset. The light intensity which permits the flies to be active must be greater in the morning than in the afternoon. The reacting material, the fly, is evidently not the same at different times of the day.

Seasonal Cycles

The distribution areas of *Drosophila pseudoobscura* and *D. persimilis* are so extensive, both horizontally and vertically, and accordingly embrace such a range of climates, that the seasonal cycles must of necessity be different in different parts of their specific areas. Systematic observations have been made by the writers on the cycles of *D. pseudoobscura* on Mount San Jacinto in California and by J. T. Patterson in Texas, chiefly at Aldrich, near Austin. The writers' observations were made in four localities, namely Andreas Canyon, Piñon Flat, Keen Camp, and Idyllwild.

The first-named locality is a palm oasis at the mouth of a perennial stream which debouches onto the Colorado Desert near Palm Springs. The elevation is approximately 800 feet. The slopes are clothed with the sparse, shrubby vegetation characteristic of the Colorado Desert. The oasis itself is made up of palms (*Washingtonia filifera*), willow (*Salix lasiolepis*), sycamore (*Platanus racemosa*), and poplar (*Populus Fremontii*). The ordinary daylight range of temperature during the winter months, except on rainy days, varies roughly from 50 to 75° F., and of relative humidity from 20 to 60 per cent. During the summer months, the site comes under the influence of the desert drought, although this effect is ameliorated in the immediate vicinity of the stream because of the tree cover. The ordinary daylight range of temperature then varies roughly from 65 to 95°, and of relative humidity from 20 to 60 per cent.

The second locality, Piñon Flat, is found on the desert side of the mountains at an elevation of 4000 feet. The climate shows greater extremes of temperature than at Andreas. Light snowfall is occasional in winter; the ordinary range of daylight temperature is from 40 to 65° F., and of relative humidity from 20 to 50 per cent. The corresponding ranges in summer are

60 to 90° and 20 to 60 per cent. The vegetation is an open woodland of piñon (*Pinus monophylla*) and juniper (*Juniperus californica*) interspersed with scrub oak (*Quercus dumosa*) and *Rhus ovata*. A thin layer of duff is found beneath the pines and oaks.

The third locality, near Keen Camp (Hurkey Creek), lies at an elevation of 4300 feet at the lower margin of the yellow pine zone. The principal cover is an open but well developed forest of *Pinus ponderosa* with shrubs of *Artemisia tridentata, Ceanothus cuneatus,* and *Rhamnus californica*. The duff is fairly thick, especially around the bases of trees. Rainfall is higher than at Piñon Flat, and several inches of snow cover the forest floor during the winter. Observations of temperature and humidity have been made only from May to November, inasmuch as the flies are not found during the winter months, unless perhaps on exceptionally warm days. During this period the ordinary range of daylight temperatures is from 40 to 75° F. in November

TABLE 5

OCCURRENCE OF *Drosophila pseudoobscura* IN DIFFERENT MONTHS

Locality	J	F	M	A	M	J	J	A	S	O	N	D
Andreas Canyon	–	x	X	X	x	·	·	·	–	–	–	–
Piñon Flat	–	x	x	X	X	x	·	·	–	–	–	–
Keen Camp	o	o	o	–	x	X	X	x	–	–	–	o
Idyllwild	...	...	...	...	x	X	X	x	...	...	...	...
Aldrich	172	131	512	1113	562	2	6	0	1	62	144	231

· few flies or none.
– fairly abundant.
X maximum.
x increasing to or decreasing from the maximum.
o unknown, but probably none or only occasional.

and May and from 50 to 90° in July and August. The corresponding humidity is 25 to 80 per cent.

Idyllwild, at an elevation of 5300 feet, is located well within the yellow pine forest, the principal trees being *Pinus ponderosa, Libocedrus decurrens, Quercus Kelloggii,* and the most abundant shrubs species of *Arctostaphylos*. It lies on the coastal side of the mountains, with a general exposure to the west. The climate is in general similar to that of Keen Camp, but being at a higher elevation and more subject to coastal influences, Idyllwild has a greater rainfall and snowfall, and the relative humidity is generally higher.

It is apparent from the above description that the four localities form a climatic gradient up the mountain, and, as judged from the nature of the vegetation, a gradient which roughly approximates the climatic gradient from the Colorado Desert northward into the Sierra Nevada. The occurrence of the flies in the San Jacinto localities, and also at Aldrich in Texas, is shown in table 5.

From this table (see also table 4 for detailed data at Andreas Canyon) it will be observed that the maximum population shifts from March and April

at Andreas Canyon to June and July at Keen Camp and Idyllwild. It is possible that at the latter station the flies persist in abundance into August as well. The data shown for "Aldrich" were obtained by systematic collecting by J. T. Patterson; the cycle suggested by his figures is similar to those of Andreas and Piñon Flat (to which his locality is more similar climatically) and somewhat intermediate between them. At the same time, his data are illustrative of the relative frequencies which we have observed at Mount San Jacinto. According to Patterson, the species is relatively uncommon in Texas. Two trips to central Mexico, made by the senior author in September (end of the rainy season) and in March (the dry season), showed the population at the former time to be only slightly less than at the latter. At Wildrose Canyon (Panamint Range, Death Valley), large numbers of flies have been repeatedly obtained in May and early in June, but only a few flies were found later in June and in early October. Although comparable in climate and vegetation with Piñon Flat, this station lies at an elevation of 7900 feet and is under snow in winter.

Although the seasonal maxima are relatively constant with reference to the time of year, they fluctuate from year to year in numbers caught, and hence presumably in population density. Climatic factors seem clearly causative of this type of fluctuation. The degree to which the population of a given region seemingly contracts and expands is apparently a function partly of rainfall. The winter of 1940–1941 was unusually wet. Not only was *D. pseudoobscura* relatively plentiful on the Colorado and Mojave deserts during the late winter and spring, being collected there many miles from tree vegetation, but at Piñon Flat, for example, the population was still abundant in July and even in August. On the other hand, the winter of 1941–1942 was more than usually dry and was followed by a dry summer during which the flies were quite scarce in July at Piñon Flat.

Abundance of flies at a given season does not necessarily mean that the flies are breeding at that time. At first glance, as was pointed out above, it seems improbable that sufficient suitable places could be found in summer in the dry forests of southern California for the larvae to exist long enough to mature. The fact that adult flies find sufficient food almost daily during this period might or might not mean that the source of supply is such that the larvae could also feed. Fortunately, we have direct proof that flies breed throughout the summer. On June 9, 1941, 2000 laboratory-grown flies homozygous for the recessive mutant gene orange (bright-red eye color) were liberated at Keen Camp. During the following week many orange-eyed flies visited the traps which had been exposed in the vicinity of the point of release; copulating pairs were observed which consisted of orange or wild, and of both orange and wild partners. Traps were exposed again from July 23 to August 8 in the same neighborhood, and during that time 41 orange-eyed flies were collected. These orange flies, however, were not the survivors of the flies released in June, but young individuals which had hatched in the wild; their age was established by inspection of their reproductive organs (see below). Again, on June 16, 1942, 3297 orange flies were released, this time at

Idyllwild. Many orange and mixed copulating pairs were seen during the following week. On July 12 to 15, traps were exposed about 400 meters from the point of release, and 5 young orange flies were captured.

The age of a fly can be judged to a certain extent by its appearance. Flies less than 12 hours old are pale, with bright eyes and semiopaque wings. Such flies never come to traps. Old flies differ from younger ones in having some of the macrochaetae broken, the edges of the wings torn, and the abdomens shriveled. Such flies are observed from time to time. The condition of the reproductive organs, however, is a better measure of the biological age than the external appearance. When females are hatched their ovaries consist of the terminal chambers only; this we shall refer to as age I. At temperatures around 22° C. and with ample food, growing oöcytes appear in a day or two (age II), and mature eggs on the 3d to 7th day. Ovaries of florid females 3 to 20 days old (age III) are loaded with mature eggs, but in old females most

TABLE 6

AGE OF FLIES COLLECTED AT IDYLLWILD, CALIFORNIA

Date	Females				Males			
	I	II	III	IV	I	II	III	IV
June 3	0	10	32	0	0	20	3	0
June 9	0	15	14	0	1	12	3	0
June 17	2	6	13	0	2	22	3	1
June 19	3	27	16	1	8	37	7	0
July 5	2	23	25	4	3	14	29	2
July 15	1	16	45	1	1	7	22	0
July 24	4	21	22	0	3	33	37	0

egg strings have regressed and only a few mature eggs are present (age IV). From the time of hatching to about 4 days, males have transparent orange-red, broadly ellipsoid testes (age I). During the following week or two, the testes elongate but remain orange-red (age II); elongation progresses and a dark-red opaque coloration develops, first in spots and then over the whole organ (age III). Males a month old have sickle-shaped dark-red testes (age IV). The speed of these changes depends on temperature, food, and probably other factors. Starving females may not have ripe eggs when 10 days old. The characters just described measure the biological rather than the chronological age, especially in females. Nevertheless, a young fly is distinguishable from a florid or an old fly. Samples of flies were collected from time to time at Idyllwild in the summer of 1942 for inspection of the external characters and of the reproductive organs. The data are summarized in table 6.

The rapid dwindling of the numbers of orange flies captured on successive days after their liberation suggests that the average longevity of the flies in nature is very much less than their longevity under laboratory conditions. This fact and the age determinations, despite all the uncertainties of the latter,

make the conclusion inescapable that young flies constantly appear through-out the summer, at least at Idyllwild and at Keen Camp. The apparent scarcity of the flies in midsummer at Andreas and at Piñon Flat, however, raises the question whether they breed in midsummer at these localities as well. Since the summer temperatures there are high, the intake of traps should be a fair measure of the population density. It is conceivable, however, that too high a temperature and too low a humidity may cause the flies to be quiescent, just as temperatures below 50° F. are known to do. Some observations suggest that this may indeed be the case. Two morning and three evening collections on July 9 to 11, 1942, at Piñon Flat produced only about a dozen flies. On July 15 a local cloudburst drenched the locality. The evening collection on July 17 produced 199, and on July 18, 151 flies in 61 traps. Were most of these flies present before the rain? Dissection of a sample of flies caught on the 18th has made this extremely doubtful: among the females 2 were of age I, 12 age II, and 9 age III; among the males 7 were of age I, 12 age II, and 9 age III. At least some of the wild flies were freshly hatched. These observations were made in connection with experiments, to be described, in which orange-eyed flies were released and their capture was attempted on the days following. The proportions of orange flies recaptured were abnormally small, before as well as after the rain referred to, but those which were found had traveled farther from the point of release than they had traveled at lower temperatures in corresponding experiments at Idyllwild. This fact suggests that the flies are not completely quiescent at Piñon Flat during the summer, and it appears probable that rain somehow hastens the hatching of the flies from pupae. A spurt in the abundance of flies after a rain has also been observed at Keen Camp (August 1941), and many of the flies which appeared after the rain were shown by dissection to have been very young.

The number of generations per year is difficult to determine. In the labora-tory a fly may remain alive long enough to meet not only its children but even its grandchildren; nevertheless we have evidence that the longevity of a fly in nature is usually only a fraction of its potential life span. At least in California, the temperatures of the habitat change greatly from day to night; precisely what these temperatures are is unknown, and the duration of the fly's development at fluctuating temperatures is also conjectural, since labora-tory experiments are usually made at constant temperatures. Under such conditions, the estimates of the number of generations can at best be only approximate. Assuming the length of a generation under summer conditions at Keen Camp or Idyllwild to be 3 weeks at the minimum, and in spring and autumn 4 to 6 weeks, the flies can hardly produce more than seven gener-ations per year in these localities, and probably less. If the breeding at Andreas Canyon is continuous throughout the year, ten generations per year in that locality is not an unlikely estimate; about half of these generations would develop during the summer shrinkage of the population. Since even in natural habitats, however, the flies may live for several weeks, the average number of generations per year may be only half of the above estimates.

MIGRATION

Any species, race, or genotype tends to increase its distribution area. In the case of *Drosophila,* the movements of the adult fly (the movements of larvae are negligible) may cause an individual to leave its progeny at some distance from the place where this individual itself was born. The distance probably varies from individual to individual and from species to species, but no matter how small it may be in one generation, the progeny of a pair, if it survives, will spread in the course of time. Moreover, from time to time some individuals may be transported passively, by wind or other agencies, over distances far greater than those which an individual could cover by means of its own organs of locomotion. Although the net result of both active and passive migration is to increase the distribution area, the two processes must be studied by different methods, because of intrinsic differences between them. The active spread produces a constant pressure on the boundaries of the distribution area, but an ecologically unsuitable barrier may cancel the result of this pressure. Passive migration is probably irregular and sporadic, but it may suddenly accomplish conquests of large areas inaccessible to active spread. Considered historically, migration also presents two different aspects. In terms of short intervals of time a species may be very sedentary, and yet it may be capable of spreading widely over long periods; on the other hand, relatively mobile forms may have their distributions fixed by specialized adaptation to conditions which exist only in a geographically limited area.

Some information is available on the passive transport of *Drosophila.* Glick (1939) in Louisiana has collected insects from an airplane at different altitudes. He records one specimen of *D. melanogaster* at 200 feet, 1 specimen of an undetermined *Drosophila* at 200 and 2 at 1000 feet, 5 specimens of *Scaptomyza adusta* (a representative of Drosophilidae) at 200, 1 at 500, 2 at 1000, and 1 at 3000 feet, 5 specimens of *Scaptomyza* sp. at 200, 3 at 1000, 2 at 2000, and 1 at 3000 feet, and 10 specimens of undetermined Drosophilidae at 200, 3 at 500, 2 at 2000, and 1 at 3000 feet. Whether or not these insects were alive at the time of capture is unknown, and if they were, they might or might not have been capable of reproduction after their aerial journey. Although no *D. pseudoobscura* or its relatives were recorded (these species do not occur in Louisiana), their passive transport by wind is nevertheless a possibility. There is also indirect evidence that this possibility is to be reckoned with, at least in terms of historical spread of the species. As was stated above, *D. persimilis* is common at intermediate and high elevations in the Sierra Nevada. But this species has also been found in the Coso Range and in a part of the Panamint Range, both of which lie to the east of the Sierra. These ranges are typical desert mountains, and their environment is not at all characteristic of the territory inhabited by *D. persimilis.* Other ranges in the Death Valley region are inhabited by *D. pseudoobscura* but not by *D. persimilis.* Deep desert valleys lie between the Sierra Nevada and the Coso and Panamint ranges. One can suppose either that *D. persimilis* in the Coso and Panamint ranges is a relic

of more continuous distribution in the remote past, or that this species is occasionally blown by winds eastward over the Sierra Nevada, where it is common, and has succeeded in establishing a few outposts on the desert ranges of the Death Valley region, the environment of which is on the whole adverse to the welfare of this species.

N. W. and E. A. Timofeeff-Ressovsky (1940a, b, c) have been the pioneers in experimental studies on rates of active migration in species of *Drosophila*. The technique used by these investigators has been to release known numbers of laboratory-grown individuals of *D. melanogaster* and *D. funebris*, marked by easily identifiable mutant characters, at the center of a rectangular experimental field measuring 70×90 or 110×110 meters. On the first and the following days after the release of the marked individuals, from 63 to 121 baited traps have been exposed checkerboard fashion around the point of release, and the marked and the wild flies which came to these traps have been recorded and again released at the point of capture. The rate of movement in *D. melanogaster* and *D. pseudoobscura* proved to be so low that experimental fields of the sizes indicated above were sufficient to contain all, or at least a majority, of the released flies for up to two weeks.

Experiments on migration rates in *D. pseudoobscura* have been conducted in the summers of 1941 and 1942 at Keen Camp, at Idyllwild, and at Piñon Flat, Mount San Jacinto, in collaboration with Bruce Wallace, Harlan Lewis, Alexander Sokoloff, Mrs. N. P. Dobzhansky, Miss R. Mirsky, and others. The resulting data, together with a mathematical analysis by Sewall Wright, will be published elsewhere; here only a summary of the conclusions reached to date can be given. The experiments were started with the technique of Timofeeff-Ressovsky only slightly modified, but this technique proved to be completely unsuitable for our species. The released marked flies (the mutant orange, which produces a bright-red eye color, was used in most experiments; in other experiments wild flies were caught, marked with a tiny spot of "platinum" nail polish on the thorax, and released again) reach the margins of an experimental field 70×70 meters in size, and pass beyond the margins, in one day after the release. Fields four times this size (140×140 meters) were tried without success. *D. pseudoobscura* is evidently much more mobile than its congeners studied by the Timofeeff-Ressovskys. The reason why all the released flies must be contained within the perimeter of an experimental field is simple: the rates of the fly's movements are arrived at by computing the variances of the distributions of the marked flies on the field. If some flies escape beyond the confines of the field, the variances will be grossly underestimated. Owing to the limitation in the number of observers, the checkerboard-like plan of the experimental field had to be abandoned. Instead, from 60 to 70 traps were arranged in two lines intersecting at right angles in the middle; the marked flies were released at the intersection. With traps spaced 20 meters apart, such cross-shaped experimental fields were built with arms up to 340 meters long. The marked flies, however, reached the ends of the arms of the cross in a few days after the release. As soon as this happened,

the plan of the experimental field was modified: two of the four arms of the cross were sacrificed and the other two arms were extended by adding traps at their ends. Linear files of traps up to 1080 meters long were built in some experiments.

Theoretically, the movements of the released marked flies in a uniform two-dimensional medium may be expected to obey one of the three following rules: (1) The flies may move at random, somewhat in the fashion of particles undergoing Brownian movement: the direction of motion during a given time interval will be independent of the direction during the preceding or the succeeding time intervals. If so, the variance of the distribution of the flies on the experimental field should increase in proportion to the time elapsed after the moment of their release at the center of the field. (2) The flies may move away from the densely populated areas into the more sparsely populated ones, or vice versa. Since in most experiments 2000 to 4000 marked flies were released at one point, the central part of the experimental field is temporarily overpopulated. If the flies can discern population density gradients and direct their movements accordingly, the variances will increase more rapidly at the beginning than at the end of each experiment, or vice versa. (3) The flies may possess a "homing instinct," known to exist in many vertebrates and also in tsetse flies among insects (Jackson, 1940). Each individual fly may establish a territory to which its movements will be largely confined. The marked flies will range more or less widely over the field until they establish their home ranges, whereupon their movements will be much more restricted. The variances will grow rapidly at the beginning of the experiment, and will be nearly stationary after the home ranges have been established.

Discrimination among the three possibilities outlined above is made difficult by disturbing influences encountered in the experiments. Outstanding among these influences are the temperature variations observed from day to day in practically every experiment. As shown by the variances of the distributions of the flies observed on different days, the flies travel much more extensively at higher than at lower temperatures. This necessitates a study of the relation between variance and temperature. The daily increment of variance increases exponentially with increase of temperature. If the logarithms of the increments of variance are plotted against the temperatures observed at the times of the maximum activity of the flies on the days when collecting has been made, the data for temperatures above approximately 60° F. seem to fall on a straight line. The few observations made at temperatures below 60° F., however, do not fall on the same line. This may mean either that some of the observations are accidentally inexact, or that the movements of the flies have different temperature coefficients below and above 60° F. Since we cannot decide which alternative is true, regression coefficients have been computed, with the aid of a method suggested by Wright, for the data including and excluding the observations at temperatures below 60° F. These regression coefficients are respectively $y = 3.13122 + 0.04950\ x$, and $y = 2.87409 + 0.0710\ x$, where y is the logarithm of the increment of variance in meters

per day, and x is the temperature in degrees Fahrenheit above 60°. The two equations give, of course, two sets of expectations for the increase of variance in the actual experiments. A comparison of the expected and the observed values leads to the conclusion that the data favor, on the whole, the hypothesis that the movements of the flies are random (the first of the three hypotheses outlined above). The third hypothesis ("homing instinct") is excluded; the second hypothesis (movement along density gradients) is unlikely, although it is possible that some slight tendency to escape overpopulated regions is present.
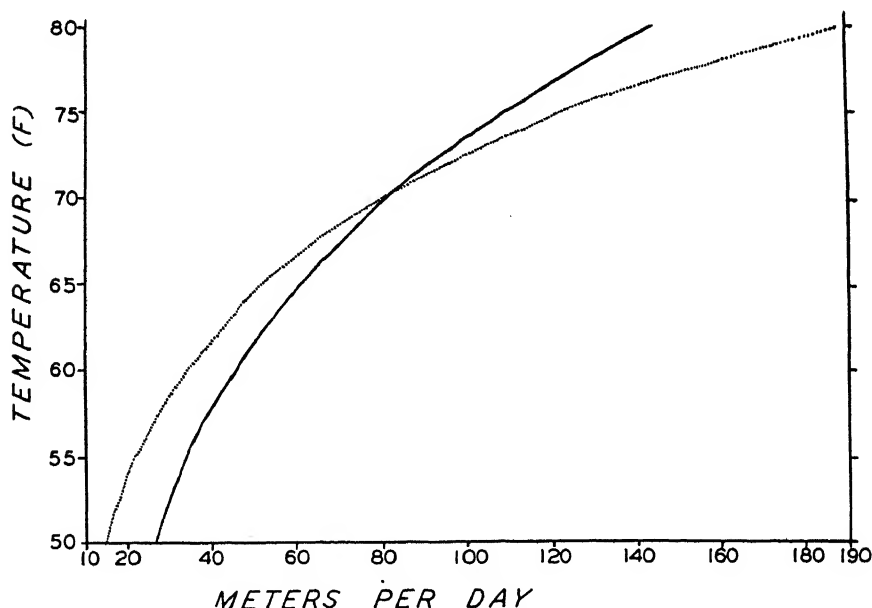
FIG. 7. The mean distances from the point of release traveled by *Drosophila pseudoobscura* at different temperatures. The two lines correspond to the two sets of expectations mentioned in the text.

The average distance traveled by the flies per day can be deduced from the daily increments of variance of their distributions on the experimental fields. As shown by Wright (unpublished), the average distance equals approximately 1.253 standard deviations per day; the standard deviation is, of course, the square root of the variance. Figure 7 presents the average distances in meters per day (abscissae) plotted against the temperatures in degrees Fahrenheit (ordinates). Two lines are shown in this figure, corresponding to the two possible sets of expectations mentioned above. At about 70° F. the two expectations coincide, indicating that the flies travel 81 meters per day on the average. At 80° the distance traveled turns out to be 144 or 188 meters; at 60°, 46 or 34 meters; and at 50°, 26 or 15 meters. The situation at the lower temperatures is obviously least satisfactorily known; this is the result of the fact that a majority of the experiments were conducted in midsummer,

when temperatures ranged around 70° F. at the times of the maximum daily activity of the flies, only a single experiment having been started at 56°.

It is plain that we have succeeded in determining at best only the order of magnitude of the daily movements of *D. pseudoobscura.* Yet even such information, inexact as it is, is valuable for an understanding of the breeding structure of natural populations. The Timofeeff-Ressovskys (1940*a, b, c*) have, unfortunately, published no data on the temperatures at which their experiments on the movements of *D. funebris* and *D. melanogaster* were conducted near Berlin, Germany. Assuming that the temperatures during their experiments were somewhat lower on the average than during ours, the conclusion is still inescapable that the distances traveled per day by *D. pseudoobscura* are ten or more times as great as those traveled by *D. funebris* or *D. melanogaster.* With similar absolute population densities per unit area, *D. pseudoobscura* will, therefore, have a larger genetically effective population than these other species. In a continuously inhabited territory there will be much less opportunity for isolation by distance with *D. pseudoobscura* than with *D. funebris* or *D. melanogaster.* Nevertheless, as compared with other insects, some of which have been observed to make flights of several miles per day, *D. pseudoobscura* must be regarded as a relatively sedentary organism. If an organism which moves at random in a uniform two-dimensional medium travels on the average a distance r per day, in n days it will have traveled on the average not the distance $rn,$ but only $r\sqrt{n}.$ Suppose, then, that at a temperature of about 70° F. individuals of *D. pseudoobscura* born or released at a given point reach in a day, on the average, the periphery of a circle with a radius of 80 meters centered on the point of birth or release. If the temperature remains constant, a circle with a radius of 160 meters will be reached in 4 days, and a circle with a radius of 400 meters in 25 days. It is to be emphasized that these are the *average* distances, and some individuals will undoubtedly move farther and others much less far from the starting point. The important conclusion is that with such rates of migration, the interchange of genes and other genetic variants between populations residing several miles apart may be slow enough to permit a racial differentiation of such populations and preservation of racial differences from swamping due to hybridization. This is, indeed, what is observed (Wright, Dobzhansky, and Hovanitz, 1942; see also part II in the present publication).

Summary

1. Three species of the *Drosophila obscura* group occur in North America. They are: *Drosophila pseudoobscura* Frolova, *Drosophila persimilis* Dobzhansky and Epling, ar.d *Drosophila miranda* Dobzhansky. *D. persimilis* is a name here proposed to designate the entity previously known as "Drosophila pseudoobscura race B." Evidence is presented to demonstrate that *D. persimilis* is, despite the paucity of structural differences, specifically distinct from *D. pseudoobscura.* Species is defined as "the stage in the process of evolutionary diver-

gence at which an array of populations once actually interbreeding or capable of interbreeding has become split into two or more reproductively isolated arrays."

2. The distribution area of *D. pseudoobscura* extends from British Columbia to Guatemala and from the Pacific Ocean to the Rocky Mountains and Texas; that of *D. persimilis,* from British Columbia to California and from the Pacific to the Sierra Nevada–Cascades mountain chain; that of *D. miranda* is confined to the Pacific coast from Vancouver Island to Monterey, with an apparently disjunct colony in the Sierra Nevada.

3. The food of the adult *D. pseudoobscura* consists chiefly of yeast and bacteria gathered probably from fermenting tree sap and similar sources. The food of the larvae is unknown, but is probably the same as that of the adult.

4. On sufficiently warm cloudless days the flies come to traps only at certain hours after sunrise and immediately before sunset. At other times they seek shelter in crevices of tree bark and similar places. The hypothesis that the diurnal periodicity is determined by changes in light intensity during the day fits the available data better than any other hypothesis which we have been able to contrive.

5. The seasonal cycles in *D. pseudoobscura* are different in different parts of its distribution region. Some of these cycles are described.

6. Experiments on the rates of active migration in *D. pseudoobscura* have been made. In reasonably uniform two-dimensional environments the flies move at random rather than follow density gradients. No "homing instinct" or "territoriality" is present. If the temperature at the time of the evening maximum of activity of the flies is close to 70° F., the average distance from the starting point traveled by the flies per day is approximately 80 meters. The migration rate grows or diminishes exponentially with changes in temperature. The observed migration rates seem to be small enough to permit racial differentiation in populations residing only a few miles apart in a continuously inhabited territory.

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II

Chromosomal Races in Drosophila pseudo-obscura and Drosophila persimilis

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CONTENTS

II

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INTRODUCTION

For more than a century systematists and anthropologists have been describing, cataloguing, and classifying races in man, in animals, and in plants. Yet despite the hundreds or perhaps thousands of investigations which have been published on this subject, the concept of race remains ambiguous. This ambiguity is inherent in the method, based on description of morphological averages, by which the problem has been approached. A racial type or standard is arrived at, which is, in effect, a system of statistical averages. Once such a type is established it becomes a tool for comparing races with one another and for deciding whether any given individual does or does not belong to the race in question. In other words, the procedure has been the same as that employed in systematic zoology and botany to delimit species and to assign a given individual to one species or another.

An implied justification of this procedure lies in the principle, the validity of which is securely established, that species evolve from races; hence species and races are assumed to be consubstantial. Another, and apparently no less valid, justification can be claimed, in that the procedure has, on the whole, stood the test of experience: systematists and anthropologists not only have succeeded in reducing the chaos of diverse racial variants to an intelligible system, but also have produced a coherent picture of the distribution and migration of many strains over the earth's surface. Nevertheless, although the method serves well as a device for the delimitation of species, it proves to be totally inadequate for the analysis of intraspecific variability.

Although it is true that species arise from races, they differ from races by virtue of the reproductive isolation of the former and the absence of such isolation in the latter. A species is a genetically closed system; species do not regularly exchange genes. Because of this fact, any given individual (species hybrids excepted) always belongs to a given species, never to two or more. Races, on the other hand, are genetically open systems. Their populations are channels through which genes can and do flow from race to race. And, because genes may vary independently from one another, an individual may carry some genes which occur frequently in the representatives of one population or race and other genes more characteristic of another. Such an individual may, in this sense, belong to two or more races at the same time; it is in fact compounded of elements of both.

To analyze and describe races adequately it is necessary to analyze and describe the distribution of the variable genes one by one. A system of morphological averages may well serve as an exploratory device, but a basic understanding of principles of racial variation can come only from knowledge of

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the distribution and relative frequencies of variable genes and chromosome structures in a population. The novelty of this technique necessitates a thorough methodological study carried out with favorable material, in order that the operational tools may be tested and perfected in the process of practical application. The variation in the gene arrangement in the chromosomes of the fly *Drosophila pseudoobscura* and its relative *D. persimilis* displays a number of features which commend it as test material for racial studies. This variation involves principally inversions of chromosome sections. The gene arrangements in the chromosomes of the salivary-gland cells can be recognized and described with precision and without undue technical difficulties. The variants resulting from inversion are perfectly discrete, a functional intermediate between an inverted and a noninverted block of genes being obviously impossible. The third chromosomes of *D. pseudoobscura* and *D. persimilis* have a further and unique advantage in that the phylogeny of the gene arrangements has been established with a degree of probability certainly equal to and perhaps higher than that of any other phylogeny. Thus, in these organisms an approximate understanding of the phylogeny, which is one of the final goals of racial studies, is available at the outset.

It is not contended herein that the techniques which have been developed for the study of chromosome structure in *Drosophila* can be adapted directly to the racial study of other organisms. *Drosophila* may be a special case. But it is hoped that the general principle of the description of populations in terms of the relative frequencies of their genetic variants will prove to be widely applicable.

Acknowledgments

Material and Technique

Between 1932 and 1942 population samples of *Drosophila pseudoobscura* and *D. persimilis* have been taken throughout the major part of the distribution areas of these species, from British Columbia to Guatemala, and from the Pacific coast to central Texas. The areas least adequately sampled are the Sierra Madre of Mexico and the region which includes western Colorado, northern Utah, and the adjacent parts of Nevada, Idaho, and Wyoming. The most adequately sampled areas are Texas, California, southern Nevada, and northern Arizona. At three localities, namely on Mount San Jacinto and the Panamint Range in California, and at Aldrich Place, near Austin, Texas, samples have been taken at regular and frequent intervals for two or more years. Most of the localities, however, are represented by a single sample only, the size of which is variable.

The technique of collecting the flies is as follows: In half-pint milk bottles or paper drinking cups are placed a layer of fermenting banana mush about $1\frac{1}{2}$ inches thick and a piece of paper toweling to absorb excess fluid and to provide a landing stage. Yeast is added to banana from 2 to 7 days before it is to be used as bait. A series of such traps is suspended from trees or bushes, or placed on the ground. The flies thus collected are transferred as soon as possible to empty glass vials; males and females are separated with or without etherization, and placed in vials provided with a solid culture medium and paper toweling. They are carried or mailed to the laboratory. In the laboratory, the females are placed singly in stock culture bottles, and allowed to produce offspring. Most of the females caught in nature are already impregnated and are able to deposit numerous fertile eggs without fresh copulation. Males collected outdoors are crossed to females of known laboratory strains. When the larvae are fully grown, their salivary glands are dissected, stained with acetic carmine or acetic orcein, and made into temporary or permanent slides.

A female has every chromosome in duplicate; a male fertilizing it carries every autosome in duplicate, and a single X and a single Y chromosome. By examining the chromosome configuration in a single larva among the offspring of a female collected in nature we can, consequently, determine the gene arrangements in two wild chromosomes of each kind, one of maternal and one of paternal origin. The same end can be accomplished by examining the chromosome configurations in about seven larvae from the offspring of a wild male crossed to laboratory females, provided the gene arrangement in the chromosomes of the latter is known. The reason for this number is as follows: Suppose that the wild male carries two chromosomes with different gene arrangements which we denote as *a* and *b;* the laboratory female to which this male is crossed contains two chromosomes with the arrangement *s.* Among the offspring produced, half must carry the chromosome combination *a/s,* and the other half the combination *b/s.* If we examine a single larva in this offspring, we determine either the gene arrangement *a* or *b;* examination of

two larvae will in 50 per cent of the cases probably reveal both arrangements *a* and *b,* but in another 50 per cent only *a* or only *b* will be seen; examination of three larvae raises the probability of detection of both *a* and *b* to 75 per cent, or three out of four trials; examination of seven larvae insures that in approximately sixty-three out of sixty-four trials both *a* and *b* will be detected. Similarly, if we examine the chromosomes of eight larvae in the offspring of a wild female fertilized in nature by a wild male, we have a satisfactory chance of determining the gene arrangement in four wild chromosomes (two maternal and two paternal) and thus knowing the constitution both of the female and of her mate. Since, however, a female may be fertilized in nature by more than one male, the determination of only four chromosomes in the offspring of such a female may sometimes be misleading; hence, this method is resorted to only when the sample of flies from a particularly interesting locality is very small, and when it is impracticable to obtain another more adequate sample. As a routine procedure, only two chromosomes are determined in the offspring of each wild female, and two in that of each wild male.

Overlapping Inversions and Phylogeny of Chromosome Structures

Very early in the history of genetic studies on *Drosophila melanogaster,* instances of suppression of crossing over in the hybrids of certain strains were discovered. These suppressions proved to be inherited as though determined by single dominant Mendelian factors. The review of *Drosophila* genetics by Morgan, Bridges, and Sturtevant (1925) lists a series of such factors, customarily denoted at that time as "C" factors, in all the chromosomes of *D. melanogaster,* except the small fourth. In 1926, Sturtevant demonstrated that one of these "C" factors in the third chromosome is not a single gene but actually an inverted section, that is, a change in the gene arrangement which involves rotation of a block of genes by 180°; if the normal arrangement of the genes is ABCD, the modified arrangement thus produced would be ACBD. At the same time it was found that two related species, *D. melanogaster* and *D. simulans,* differ in the inversion of a large block of genes in the third chromosome (Sturtevant and Plunkett, 1926). It was correctly assumed that most of the "C" factors not then examined in detail were likewise inversions. In 1931 Sturtevant published a systematic study of a number of strains of *D. melanogaster,* the wild ancestors of which were collected in different geographical regions of the New and Old Worlds. Although a majority of these strains proved to contain in all chromosomes the standard gene arrangement (that is, the usual arrangement with which geneticists were familiar in their experiments involving laboratory cultures), some strains carried inversions in one or the other of their long autosomes (second and third chromosomes). Inversions were thus shown to be not merely laboratory products, but present in wild populations as well.

This early work relied for the detection of inversions on the suppression of crossing over which they produced. The field of investigation was limited

to those species in which adequate linkage maps of chromosomes were available; the labor involved was a further limitation, especially if it was desired to distinguish between two or more different inversions occurring in the same chromosome. An alternative method was evolved by McClintock (1933) which was based on the formation at meiosis of "chromatid bridges" and chromosome fragments in inversion heterozygotes. This method has been widely used in favorable materials, and through its application the fact has become established that inversions are widespread in the natural populations of many plants and animals, and, possibly, in man (for reviews see Darlington, 1937; Dobzhansky, 1941*b*).

The introduction of the technique for studying the chromosomes in the larval salivary glands of *Drosophila* and other flies (Painter, 1934) has furnished by far the easiest and most precise method of detecting and studying the gene arrangements in the organisms to which this method is applicable. Because of the specific attraction between the homologous loci in the chromosomes, an individual which carries two chromosomes differing in a single inversion (ABCD and ACBD) displays a characteristic looplike configuration in its salivary-gland cells (fig. 1). Since the linear arrangement of the disks in the salivary-gland chromosomes is characteristic and the disks are recognizable, inversion homozygotes as well as heterozygotes can be identified. Inversions have now been encountered in all species of *Drosophila* which have been examined for them.

More than one inversion may occur in the same chromosome; that is, a chromosome which has been subjected to one inversion may subsequently have another section inverted. Sturtevant and Dobzhansky (1936*b*) and Dobzhansky and Sturtevant (1938) have analyzed the consequences of these multiple inversions. Four classes have been defined. Two successive inversions may be separated by a section which preserves the original gene sequence (independent inversions, ABCDEFGH → ACBDEFGH → ACBDEGFH). The second inversion may occur inside the first or may include the first (included inversions, ABCDEFGH → AGFEDCBH → AGFDECBH, or ABCDEFGH → ABCEDFGH → AGFDECBH). Two inversions may have one point of breakage in common (tandem inversions, not known with certainty to occur in natural populations but obtained in X-ray experiments, ABCDEFGH → ADCBGFEH). Finally, the second inversion may have one break inside and the other outside the first inversion (overlapping inversions, ABCDEFGH → AEDCBFGH → AEDGFBCH).

As was pointed out by Sturtevant and Dobzhansky, the overlapping inversions are of particular interest, since they permit inferences to be drawn regarding the phylogeny of the resulting gene arrangements. As an example, let us designate the arrangements ABCDEFGH, AEDCBFGH, and AEDGFBCH respectively I, II, and III. If inversions which occur in nature involve only two breaks in the chromosome, the arrangement III can arise from I (or vice versa) only through II as a connecting link. Thus, the

phylogeny of the gene arrangements I, II, and III can be I → II → III, or III → II → I, or I ← II → III, but not I → III, or III → I. Hence, if the arrangements I and III are known, it can be predicted either that arrangement II exists and remains to be discovered, or else that it has existed in the past and become extinct. Such predictions have been made and borne out by subsequent investigation (Dobzhansky and Sturtevant, 1938; Dobzhansky, 1941a).

Because many of the conclusions to be drawn from the present investigation are dependent on the inferences concerning phylogeny of gene arrangements, this argument must be carefully examined. We must consider the possibility that the same gene arrangement may have arisen repeatedly and in different ways. Thus, if the chromosome ABCDEFGH (I) should break simultaneously at four points, rather than two, namely between A and B, C and D, E and F, and G and H, the arrangement AEDGFBCH (III) might arise at one step. Even more complex transformations can be conceived; for example, ABCDEFGH → ADEFGBCH → AEDFGBCH → AEDGFBCH, and the like. Two possibilities in particular must be considered; namely, whether multiple breakages (involving more than two simultaneous breakages in a chromosome) are likely to occur in nature, and whether repeated breakage between the same two loci is likely.

Multiple chromosome breakage followed by formation of complex gene rearrangements is well known in laboratory experiments which involve treatments of *Drosophila* with heavy doses of X rays (Bauer, Demerec, and Kaufmann, 1938; Bauer, 1939; Kaufmann, 1939). Whether such multiple breakages also occur in nature is a problem which reduces itself to the question of the frequency of natural chromosome breakages in general. It is reasonable to suppose that the frequency of multiple breakage is the product of the frequencies of single breaks.

Spontaneous single breakages appear to be rather common in some organisms (e.g. in *Tradescantia,* Giles, 1940), but the following evidence, direct and indirect, suggests that it is very rare in *Drosophila pseudoobscura.* Various strains of this fly have been kept in the laboratory for several years, and their chromosomes have been examined repeatedly, yet no change in their gene arrangement has ever been observed. Even more convincing is the observed evidence from wild flies. In the course of the investigation reported in this paper, the chromosomes of considerably more than 10,000 descendants of wild parents have been studied, particular attention being paid to the third chromosomes. It is fair to say that the gene arrangement in more than 20,000 third chromosomes and a somewhat smaller number of other chromosomes has been scrutinized. If *de novo* formation of spontaneous gene rearrangements were at all frequent, it seems that some instances of new and previously unknown configurations would have been detected. Actually, not a single translocation heterozygote has been encountered. It is to be expected, of course, that translocations would be mostly eliminated in natural populations of *Drosophila* within a few generations after their appearance; nevertheless, at

least some translocations would probably have been seen if they arose at all frequently. Many inversions have been found, of course. But most of them have been observed repeatedly and in populations collected in localities often geographically remote, which suggests that these inversions have arisen in a more or less remote past and have become established as integral constituents of the populations. Inversions once regarded as unique have become familiar as more material from the proper geographical localities has become available, and among the gene arrangements known at present in the third chromosome of *D. pseudoobscura,* only four have been seen only once (see below). These are "Cochise," encountered in a small sample from the Chiricahua Mountains of Arizona; "Texas," found in a fairly small collection from Dilley, Texas; and one each from Mount St. Helena, California and from Keen Camp, California. The first three come from localities from which further samples have not been available. Only the last was found in a region the population of which is thoroughly known, and hence may be suspected of having recently appeared in that population. In addition, two of the gene arrangements in the second and one in the fourth chromosome, respectively, have been seen only once and may conceivably be of relatively recent origin. Taking into account the numbers of chromosomes examined, we feel justified in concluding that spontaneous chromosome breakage in *D. pseudoobscura* is rare, and hence that multiple breakage must be very infrequent.

Still other evidence which suggests the rarity of multiple breakage is the absence in natural populations of certain chromosome configurations which would be possible if multiple breakage were operative. Suppose the chromosome ABCDEFGH is broken into fragments A, BC, DE, FG, and H. The reunion of these fragments could produce the following twenty-five gene arrangements (in addition to complete or partial restoration of the original connections):

1. ACBDEGFH	10. AEDBCGFH	19. AFGDEBCH
2. ACBEDGFH	11. AEDGFBCH	20. AFGDECBH
3. ACBFGEDH	12. AEDFGBCH	21. AGFCBEDH
4. ACBFGDEH	13. AEDFGCBH	22. AGFCBDEH
5. ACBGFDEH	14. AEDGFCBH	23. AGFBCEDH
6. ADECBGFH	15. AFGBCEDH	24. AGFDEBCH
7. ADEBCGFH	16. AFGCBDEH	25. AGFDECBH
8. ADEGFCBH	17. AFGCBEDH	
9. ADEGFBCH	18. AFGEDBCH	

Among these twenty-five possible arrangements, only two (nos. 11 and 17) are identical with overlapping inversions which would be derived from the original arrangement by two inversion steps, neither of which involved repeated breakage of the chromosome at the same point (fig. 1). Indeed, arrangement 11 can arise as follows: ABCDEFGH → AEDCBFGH → AEDGFBCH, and arrangement 17 thus: ABCDEFGH → ABCGFEDH → AFGCBEDH. These two types of overlapping inversion can be distinguished in the salivary-gland chromosomes, as shown schematically in figure 1. Arrangement 1 repre-

sents two independent inversions, and no. 25 two included ones. The remaining twenty-one arrangements would, if they arose at once, require four simultaneous breaks, or, if only two breaks arose simultaneously, require more than two inversion steps as well as repeated breakage of the chromosome at exactly the same points. Only overlapping, independent, and included inversions, and none of the other types, have so far been detected in natural popula-
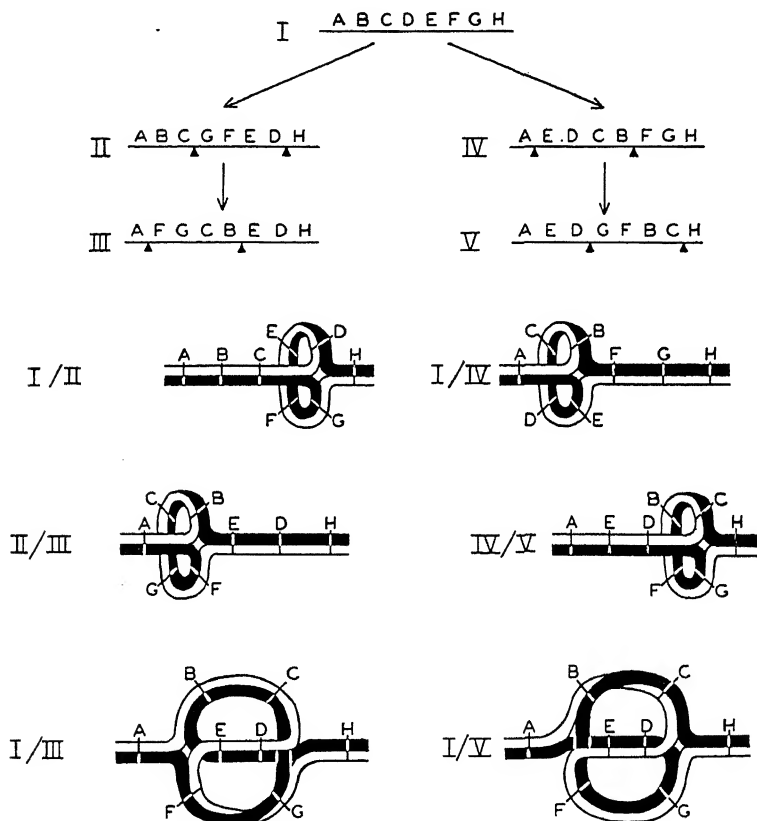
Fig. 1. A schematic representation of chromosome pairing in inversion heterozygotes. Single inversions (upper four) and double overlapping inversions (lower two).

tions. This is a strong argument against the occurrence of multiple breakage in nature.

The following arguments are also relevant to evaluation of the probability of the recurrence of breakages at the same points, giving rise repeatedly to the same gene arrangement. According to the map of the third chromosome of *Drosophila pseudoobscura* published by Dobzhansky and Sturtevant (1938), this chromosome contains more than 500 stainable disks. This number is certainly an underestimate; the right limb of the second chromosome of *D. melanogaster*, which is known to be homologous to the third of *D. pseudo-*

obscura, contains 1136 disks (Bridges and Bridges, 1939). Assuming the probability of breakage at any one locus to be uniform throughout the chromosome, the probability of repeated origin of the same inversion is between 500^2 and 1150^2.

This is a small probability indeed. But are we justified in making the assumption just stated? Can we exclude the possibility that certain points in the chromosome are more prone to undergo breakage than others, and that breakages are correlated in such a way that a fracture of the chromosome at the locus A is likely to be accompanied by a fracture at a certain other locus B? Spontaneous chromosome breakage in *Drosophila* being far too rare to furnish the necessary evidence, we must, perforce, examine the fractures induced by X rays. Bauer, Demerec, and Kaufmann (1938) and Bauer (1939) have found that in *Drosophila melanogaster* the incidence of breakage is proportional to the length of the chromosome, that the distribution of breakages within a chromosome is random (except in the heterochromatic regions), and that there is no "modal length" of the chromosome section between two breakages. Although Kaufmann (1940) has more recently described a somewhat increased probability of breakage in certain sections, which may be akin to heterochromatin in their nature, the validity of the original conclusions of the above investigators is little impaired.

It can, of course, be argued that conditions in *Drosophila pseudoobscura* are not comparable with those in *D. melanogaster.* Dobzhansky and Sturtevant (1938) have shown that in the former species the variation of the gene arrangements in the third chromosome is much greater than in any other chromosome; in *D. melanogaster* no such concentration of the variability in a single chromosome is observed. Taken at its face value, this suggests that the third chromosome of *D. pseudoobscura* is particularly prone to undergo breakage. Helfer (1941), however, has carried out experiments with *D. pseudoobscura* similar to those of Bauer, Demerec, and Kaufmann with *D. melanogaster,* and has found no indication of a high breakability of the third chromosome. On the contrary, the distribution of the observed breaks within three chromosomes proved to be relatively uniform. Furthermore, none of the inversions induced by Helfer in the third chromosome were identical with the inversions which occur naturally. As far as X-ray-induced breakages are concerned, there is, therefore, no indication of any preferential occurrence of chromosome fractures at definite combinations of loci. In the absence of any evidence to the contrary, we are obliged to conclude that a repeated origination of the same inversion at different times and places is at least highly infrequent.

Nevertheless, the reason why the third chromosome shows a greater variability in gene arrangement than the other chromosomes remains obscure. One might conjecture that many, or most, gene arrangements which arise are eliminated in natural populations because of the decreased viability which they produce, and that such position effects may be less frequent in the third than in the other chromosomes. This conjecture is, however, as yet devoid of factual basis.

ANALYSIS OF GENE ARRANGEMENTS

As was stated above, all variant gene arrangements thus far detected in natural populations of *Drosophila pseudoobscura* and *D. persimilis* can be explained as the result of inversions of chromosome segments in the course of phylogeny. Examination of the chromosomes in the larval salivary-gland cells is the most efficient method of investigating them. The gene arrangements are most conveniently described by comparison with a normal or standard arrangement. In *D. pseudoobscura* and *D. persimilis,* the gene arrangements in the two limbs of the X chromosome and in the second, fourth, and fifth chromosomes are relatively constant, one configuration of each being common throughout the distribution area. These common arrangements have been designated as standards. In the third chromosome the gene arrangement is so highly variable that there is not a single arrangement which can be regarded as normal for either species as a whole. The choice of a standard arrangement in the third chromosome is, therefore, arbitrary. An arrangement common in populations of *D. pseudoobscura* residing on the Pacific coast was chosen, and is known as Standard. The gene arrangements in *D. persimilis* can easily be derived from the Standard.

Following the example set by Bridges (1935) in *D. melanogaster,* the salivary-gland chromosomes of *D. pseudoobscura* have been subdivided into 100 sections numbered from 1 to 100. The left limb of the X chromosome (XL) contains sections 1–17, the right limb (XR) includes sections 18–42, the second chromosome 43–62, the third 63–81, the fourth 82–99, and the small fifth chromosome is the section 100. The first orientation maps of all the chromosomes were published by Tan (1935). More satisfactory maps were later published by Dobzhansky and Tan (1936) and by Tan (1937), and an improved map of the third chromosome is to be found in Dobzhansky and Sturtevant (1938). The reader is referred to that paper. In this map, again following the example of Bridges, the numbered sections have been split into divisions denoted by letters. The third chromosome contains 68 divisions.

Not only different chromosomes but also sections of the same chromosome in the salivary-gland cells can be identified by their disk patterns, despite the fact that the conformation of the separate disks and groups of disks varies to some extent from cell to cell. For example, the inflated proximal part of section 80 in the third chromosome may appear completely unbanded (see Tree Line / Chiricahua in plate 2), or it may have a dozen faint but regular disks (Standard / Pikes Peak, plate 1), or it may contain a diffuse darkly staining area (Cuernavaca / Standard, plate 1). Other regions are relatively constant in appearance, and serve as landmarks for recognition. For example, the basal part of section 73 contains a symmetrically arranged group of disks, among which the two outer doublets stand out clearly in almost every cell; the distal part of 80 has four heavy doublets; the basal part of 72 has a group of very heavy disks frequently fused into a single dark mass (compare the different drawings in plates 1–4). An experienced observer can, without question,

identify a chromosome fragment several sections long, and even much shorter fragments are frequently identifiable.

No matter how complex an inversion configuration may appear, there is always one and only one possible interpretation which fits it. Take, for example, the Pikes Peak / Cuernavaca configuration represented in plate 3. Since any inversion configuration is formed by pairing of two chromosomes which contain the same loci arranged in different linear orders, the constituent chromosomes can be represented schematically as shown in figure 2. It is certain that this scheme is correct because any modification of it would make one of the paired chromosomes include parts not present in the other. The chromosome strands are now marked with letters, using at least two letters for each paired section (figure 2). The drawing in plate 3 does not show
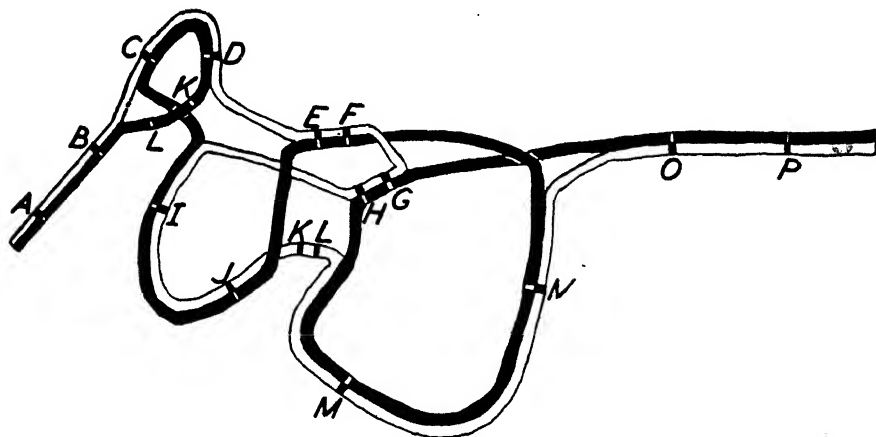
Fig. 2. Chromosome pairing in heterozygotes carrying Pikes Peak and Cuernavaca gene arrangements. This is a schematic representation of the configuration shown in plate 3.

very clearly that the homologue of the section KL in the black strand in figure 2 is located in the white strand between J and M. This fact has been established by examining figures other than that reproduced in plate 3. The white strand contains, then, the letters from A to P arranged in alphabetic order. The black strand is ABLKDCIJEFNMHGOP. How might these arrangements be derived from each other? If it is true that the probability of repeated breakage of a chromosome at the same point is small and negligible, one must postulate three connecting links between the arrangements observed, as follows:

Cuernavaca: ABCDEFGHIJKLMNOP
I: ABCDEFNMLKJIHGOP
II: ABCDKLMNFEJIHGOP
III: ABLKDCMNFEJIHGOP
Pikes Peak: ABLKDCIJEFNMHGOP

It happens that among the three arrangements here postulated, the arrangement I is found in nature, and is known as the Santa Cruz arrangement; the

arrangement III is also found, and is known as the Standard; the arrangement II has never been found, and remains Hypothetical (see below). Thus, by comparing the Cuernavaca and Pikes Peak arrangements we can, by deduction, describe other arrangements. In the example just analyzed it was necessary to postulate that the chromosome had been broken twice near C, once in the transition from II to III and again in the transition from III to Pikes Peak. In other words, the Hypothetical and Pikes Peak inversions are not clearly overlapping (see below). Every one of the configurations represented in plates 1–4 can be analyzed along similar lines, and the results of the analyses make a consistent story.

DESCRIPTION OF GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF DROSOPHILA PSEUDOOBSCURA

Dobzhansky and Sturtevant (1938) have described eleven gene arrangements in the third chromosome of *Drosophila pseudoobscura,* and five in *D. persimilis;* one arrangement, the Standard, is common to the two species. Since 1938, several new arrangements have been identified and those previously known have been re-examined more carefully, with the result that some mistakes in the original descriptions have become apparent.[1] Some of the gene arrangements are widespread, others are endemic to a restricted locality. The former are kept in stock in the laboratory at Columbia University, and are described in detail below; the latter are less adequately known.

In addition to Standard, nine gene arrangements in *D. pseudoobscura* and four in *D. persimilis* have been studied in detail. Not counting the homozygotes, these arrangements are capable of forming ninety-one combinations. Only a part of the combinations have actually been examined, namely those that are likely to occur in natural populations and those in which the constituent arrangements differ in a single inversion. With one exception, all the drawings in plates 1–4 have been made from single cells with the aid of a camera lucida. The exception is the configuration Standard / sex ratio in the XR chromosome of *D. pseudoobscura* (pl. 4), which is a composite drawing. Cells were chosen for illustration which showed the respective configurations most clearly and the homologous sections paired most completely. The parts of the chromosomes which failed to show clearly their disk patterns are represented in the drawings by outlines only. Figure 3 shows the sequence of sections and divisions in the nine gene arrangements in *D. pseudoobscura* which were studied in detail. The heavily underscored parts of the chromosomes in figure 3 are those which have become inverted in the formation of a given gene arrangement from its putative ancestor, the Standard arrangement being assumed to represent the prototype.

The names of the gene arrangements have been taken from the localities in which the respective arrangements were first encountered. If two arrange-

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[1] The cytological part of the Dobzhansky and Sturtevant (1938) paper was prepared by Dobzhansky, who is, therefore, alone responsible for the mistakes therein.

STANDARD

ARROWHEAD

HYPOTHETICAL

PIKES PEAK

SANTA CRUZ

CHIRICAHUA

CUERNAVACA

TREE LINE

OLYMPIC

OAXACA

ESTES PARK
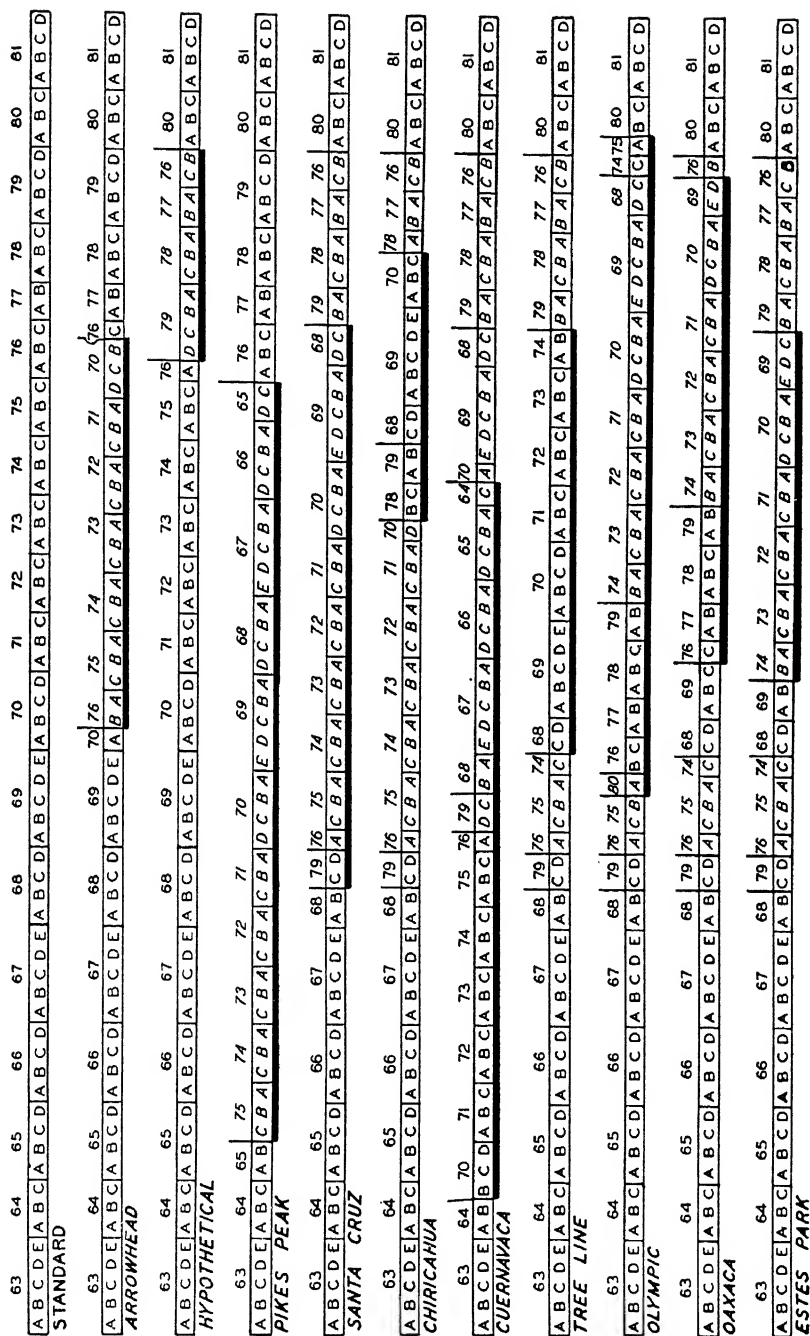
Fig. 3. The principal gene arrangements in the third chromosome of *Drosophila pseudoobscura*, in terms of the sections and subdivisions of the standard map.

ments were found in the same locality, they were formerly distinguished by numerals I and II (thus, Sequoia I and Sequoia II in Dobzhansky and Sturtevant, 1938). This complication is now avoided by giving a separate name to each arrangement. This system of naming is by no means perfect, but alternative systems have proved even less satisfactory. The following gene arrangements are known in *D. pseudoobscura* in addition to Standard:

Arrowhead

Discovered in a sample from Arrowhead, British Columbia. Differs from the Standard by a single moderately short inversion. To obtain the Arrowhead arrangement from the Standard, the Standard chromosome must be broken in sections 70B and 76B, and the intervening segment (i.e., sections 71, 72, 73, 74, 75, and parts of 70 and 76) inverted. The hybrids Standard / Arrowhead have a short inversion loop which is frequently paired fairly completely. In plate 1 there are two drawings which represent the Standard / Arrowhead configuration; they are designed to convey an idea of how different the same configuration may appear in different cells. In one of these drawings the part of the chromosome distal to the inversion is stretched (sections 77, 78, and 79) while the inversion itself is relatively contracted. In the other drawing sections 78 and 79 are contracted. Standard / Arrowhead heterozygotes are very common in many natural populations.

Pikes Peak

Discovered on Pikes Peak, Colorado. Differs from Standard by a long inversion, embracing sections from 65C to 75C inclusive (fig. 3). The Pikes Peak / Standard hybrids have one inversion loop (pl. 1), which frequently shows a considerable number of unpaired segments near the inversion breaks. The distal break in Pikes Peak is clearly different from the distal one in Arrowhead; the part intervening between the two breaks contains two heavy doublets of section 76B and the relatively faint disks of 76A. The Arrowhead and Pikes Peak inversions are, therefore, overlapping. The Arrowhead / Pikes Peak heterozygotes (pl. 3) have two large inversion loops and a short piece (76A and 76B) which has never been observed to pair with its homologue. This configuration is very common in natural populations. In accordance with the theory of overlapping inversions, the descent must have been:

Arrowhead ⟷ Standard ⟷ Pikes Peak

Santa Cruz

Predicted on the basis of a comparison of the Tree Line and Standard arrangements, and subsequently identified from a population sample from Santa Cruz Island, off the coast of California (Dobzhansky and Sturtevant, 1938). The Standard / Santa Cruz heterozygotes have a rather complex pair-

ing configuration, consisting of two inversion loops (pl. 1). The distal one is rather short and includes sections 76B to 79B; the longer proximal one includes sections 68C to 76A. If Santa Cruz differed from the Standard by two tandem inversions, the divisions 79C and 79D would be found lying between 79B and 68C. Actually these two short divisions can be seen intercalated between 68B and 76A, adjacent to the basal part of the larger inversion loop; they fail to pair with their homologue in the Standard strand (pl. 1 and fig. 3). This fact, carefully ascertained in many figures, proves that Santa Cruz arose from Standard through a hypothetical intermediate step. This Hypothetical, and as yet undiscovered, arrangement must have had the order of sections shown in figure 3. It arose from the Standard (or vice versa) by breaks between 79D and 80A and in 76A, and by inversion of the intervening segment. The Hypothetical arrangement was then broken distal to the heavy disk which separates 68B and 68C and in 79B, close to the boundary with 79C. This second inversion gave rise to the Santa Cruz arrangement. The phylogeny is as follows:

$$\text{Standard} \longleftrightarrow \text{Hypothetical} \longleftrightarrow \text{Santa Cruz}$$

There is no doubt that the proximal break of the Hypothetical inversion lies proximally to the distal break in Arrowhead; the common piece is very short but is clearly identified by the heavy doublets of 76B. Arrowhead and Hypothetical are overlapping. The distal break in Pikes Peak and the proximal one in Hypothetical are very close to each other, but there seem to be several light disks which are involved in neither inversion (cf. Dobzhansky and Sturtevant, 1938). These inversions are, therefore, independent. Theoretically, Hypothetical could have arisen from a Pikes Peak chromosome, or vice versa, the two inversions subsequently separating by crossing over with a Standard chromosome. In view of the shortness of the intervening piece, such a sequence of events is so extremely unlikely that the alternative relationship of Hypothetical and Pikes Peak through Standard is practically certain. The inversion which transformed Hypothetical into Santa Cruz involves most of the chromosome parts included in Arrowhead, but the position of sections 79C and 79D excludes any possibility of a direct relationship between the two. The combination Santa Cruz / Arrowhead (pl. 2) occurs frequently in nature. It is a fairly complex and variable configuration. The condition represented in plate 2 is attained in a minority of cells, since sections 69 and 70A frequently fail to pair. If they do not pair, the chromosome straightens out and shows only a short subterminal inversion (corresponding to Hypothetical) and extensive unpaired segments close to the middle of the chromosome length. Sections 79CD and 76B have never been observed to pair with their homologues. The configuration Pikes Peak / Santa Cruz has been obtained in the laboratory; it reminds one somewhat of the Arrowhead / Pikes Peak figure, but there are many unpaired sections and a subterminal inversion is present (corresponding to Hypothetical).

Chiricahua

Named Chiricahua I in Dobzhansky and Sturtevant (1938) and in Dobzhansky (1937a, 1941b). Discovered in the Chiricahua Mountains, Arizona. Derived from Santa Cruz by fractures close to the middle of 70D and in 78B, and the inversion of sections 70, 69, 68CD, 79AB, and 78 (fig. 3). Chiricahua / Santa Cruz heterozygotes have a rather short inversion close to the distal end of the chromosome (pl. 2), which is so characteristic in its position that it can very easily be distinguished from any other configuration. On the other hand, the Chiricahua / Standard configuration (pl. 1), which is common in natural populations in California and elsewhere, is very involved and is difficult for a beginner to analyze. Many cells show three rather short inversion loops, the connections between which are sometimes difficult to follow. The frequent failure of sections 69 and 70 to pair transforms this figure into a configuration superficially very distinct: a single inversion loop close to the middle (sections 71 to 75), and long unpaired segments above and below that loop. Both configurations may occur, of course, in different cells of the same gland. Complete pairing of all homologous sections has never been observed; sections 76 and 77 are practically always unpaired. The combination Chiricahua / Arrowhead (pl. 3) appears no more complex than Chiricahua / Standard, although the former contains a quadruple and the latter only a triple inversion. This is because the inversion transforming Standard into Arrowhead is somewhat similar to that changing Hypothetical into Santa Cruz. The frequent failure of sections 69 and 70 to pair in Chiricahua / Arrowhead allows the chromosome to straighten out completely; such a straightened chromosome has no inversion loops left in it, but has many unpaired sections, reminding one of deficiency or duplication configurations. Finally, if most sections are paired, Chiricahua / Pikes Peak heterozygotes have one of the most complex configurations found in the course of the present investigation (pl. 3). It is comparable in complexity with chromosome configurations encountered in the interspecific hybrids *Drosophila pseudoobscura* × *D. miranda* (Dobzhansky and Tan, 1936). Nevertheless, this configuration has been found in certain natural populations of western Texas. In many individuals this pairing is, of course, incomplete. The inversion which transforms Hypothetical into Santa Cruz clearly overlaps that which accomplishes the transition from Santa Cruz to Chiricahua. Hence, the phylogeny is undoubtedly:

$$\text{Hypothetical} \longleftrightarrow \text{Santa Cruz} \longleftrightarrow \text{Chiricahua}$$

Cuernavaca

Discovered in the mountains above Cuernavaca, Morelos, Mexico. Cuernavaca / Santa Cruz heterozygotes have a single long inversion loop which includes more than one-half of the length of the chromosome (pl. 2). This configuration has a superficial resemblance to that of Standard / Pikes Peak heterozygotes (pl. 1), but the two are easily distinguishable because the former

has the dark disks of sections 76 and 77 adjacent to the bulb of section 80 and has the dark part of section 65 included in the inversion. Cuernavaca may have been derived from Santa Cruz by a single inversion with breaks in 64C and 70A (fig. 3). This inversion broadly overlaps those transforming Hypothetical into Santa Cruz and Santa Cruz into Chiricahua. The phylogeny is clearly:

Hypothetical ⟷ Santa Cruz ⟷ Cuernavaca, and

Chiricahua ⟷ Santa Cruz ⟷ Cuernavaca

The configuration Cuernavaca / Standard (pl. 1) seldom, if ever, occurs in nature. It is complex but not so difficult to analyze as Chiricahua / Standard. Sections 68 and 69 in Cuernavaca / Standard fail to pair in most cells (see this configuration in Dobzhansky and Sturtevant, 1938). The configuration Cuernavaca / Pikes Peak has been discussed above (fig. 2). In most cells sections 65, 68, and 69 fail to pair; in fact, the relative completeness of pairing illustrated in plate 3 is exceptionally high.

Tree Line

First encountered in a population sample from tree line (about 11,000 feet) on Pikes Peak, Colorado. This is an important arrangement because the line of descent from Santa Cruz to Olympic, Estes Park, Oaxaca, and Hidalgo passes through it. The heterozygotes Tree Line / Santa Cruz have a moderately short inversion (pl. 2) which has a superficial resemblance to that in Standard / Arrowhead heterozygotes (pl. 1). The two are easily distinguishable because in Tree Line the landmarks of sections 76 and 77 are adjacent to the bulb of section 80. Santa Cruz is transformed into Tree Line by an inversion with breaks at the dividing line of 74B and 74C and between 79B and 68C (fig. 3). Comparison of the Hypothetical / Santa Cruz and Santa Cruz / Tree Line inversions (fig. 3) shows that the two are apparently not overlapping, but the latter is included in the former with the distal breaks coinciding. One could, therefore, visualize the phylogeny according to either of the two following courses:

Hypothetical ⟷ Santa Cruz ⟷ Tree Line

Hypothetical ⟷ Tree Line ⟷ Santa Cruz

The former course demands only two simple inversions, and the intermediate step, Santa Cruz, is known to exist in nature. But in order to transform the Hypothetical arrangement into Tree Line directly, one must assume that the chromosome is broken at three places, namely between 68B and 68C, between 79B and 79C, and between 74B and 74C. The chromosome segment 74C, 75, 76A, 79DC must then be intercalated, in inverted order, between 68B and 68C. In this way Tree Line would be obtained. Another inversion with two breaks, both of which would have to coincide with similar ones postulated for the transition from Hypothetical to Tree Line, might then transform Tree Line into Santa Cruz. The conclusion is, therefore, that the origin

of Tree Line from Hypothetical through Santa Cruz is vastly more probable than the origin of Tree Line directly from Hypothetical with a subsequent change of Tree Line to Santa Cruz.

The Standard / Tree Line heterozygotes (pl. 1) have a configuration which consists of three inversion loops. The shortest of these, including section 75 and the adjacent parts of 74 and 76, frequently fails to form, whereupon the chromosome straightens out and displays only a short subterminal inversion, corresponding to Hypothetical, and unpaired sections close to the middle of the chromosome. The Standard / Tree Line configuration may, therefore, be confused with Santa Cruz / Arrowhead (cf. pl. 2 and the description above). With a little practice, however, the two are easily distinguished. The simplest guide is to observe the positions of the landmarks of sections 72 and 73. In Santa Cruz / Tree Line section 73 is distal to 72, while in Santa Cruz / Arrowhead 72 is distal to 73. Tree Line / Chiricahua and Tree Line / Cuernavaca heterozygotes (pl. 2) give configurations to be expected from two broadly overlapping inversions. These configurations closely resemble the schematic figures in figure 1. There is no doubt, therefore, that Tree Line is indirectly related to Cuernavaca and to Chiricahua through Santa Cruz.

Tree Line / Arrowhead heterozygotes, which are frequent in natural populations, form an extremely complex chromosome configuration (pl. 3). No cell has ever been found in which a complete pairing of homologues was attained, and cells in which the entire distal part of the chromosome is unpaired are rather frequent. Nevertheless, this configuration can be recognized without much difficulty. The configuration Tree Line / Pikes Peak (pl. 3) is also common in nature; sections 74 and 75 are usually unpaired.

Olympic

Discovered in a sample from the Olympic Peninsula, Washington. A single long inversion loop is observed in Olympic / Tree Line heterozygotes (pl. 2), proving that Olympic is derived from Tree Line by breakage in the Tree Line chromosome in 75A, distal to the heavy doublet, and in 80B close to the boundary with 80A. This long inversion includes that which transforms Santa Cruz into Tree Line (fig. 3). Olympic / Santa Cruz heterozygotes have a very characteristic configuration (pl. 2) which is frequently so clear as to be almost diagrammatic. The phylogeny of Olympic, Tree Line, and Santa Cruz is uncertain. The most probable course is:

$$\text{Santa Cruz} \longleftrightarrow \text{Tree Line} \longleftrightarrow \text{Olympic}$$

but it is also possible to visualize the following alternative: By breakage in 75A and 80B, Santa Cruz might have given rise to an intermediate arrangement which, by breakages between 74B and 74C and between 79B and 68C, then produced Olympic. On this hypothesis, Tree Line might have arisen by double crossing over between an Olympic and a Santa Cruz chromosome. Such crossing over, however, would have produced, in addition to Tree Line, another gene arrangement which has never been encountered. The fact

that neither of these arrangements has been encountered makes this alternative very improbable. Nevertheless, it must be admitted that the descent of Olympic from Santa Cruz through Tree Line is established less rigorously than other phylogenies discussed above.

Olympic / Standard heterozygotes have a configuration (pl. 1) which appears simpler than it is in reality. Usually only two inversion loops are produced, but a quadruple inversion is here involved. The reason for this deceptive simplicity is the failure of short homologous sections separated by long nonhomologous ones to establish pairing association (see the position of sections 79 and 75 in the drawing in plate 1).

Oaxaca

Discovered in Cerro San José, near Oaxaca, Mexico. This arrangement is derived by a single inversion from Tree Line, as attested by the configuration found in Oaxaca / Tree Line heterozygotes (pl. 1). The breakages are located in 69D and 76B (fig. 3). The configuration in Oaxaca / Standard heterozygotes (pl. 1) is not very different from that in Olympic / Standard, but the former is more difficult to interpret on account of the abundance of long unpaired sections (the drawing reproduced in plate 1 has been made from an exceptionally clear cell).

Comparison of Oaxaca with Olympic leads to some interesting speculations. As is shown in figure 3, both sequences just named may have been derived by single inversions from Tree Line. Therefore the most probable phylogeny is:

Santa Cruz ⟷ Tree Line ⟷ Oaxaca, and
Oaxaca ⟵⟶ Tree Line ⟷ Olympic

An examination of figure 3, however, and of the configurations Tree Line / Olympic and Tree Line / Oaxaca in plates 2 and 1 shows that the inversion which transforms Tree Line into Oaxaca is included in that which transforms Tree Line into Olympic. Therefore, in theory, double crossing over between Olympic and Oaxaca chromosomes was capable of producing the Tree Line arrangement as well as another complementary arrangement not as yet found in nature. As we have seen above, Tree Line might also have conceivably arisen by double crossing over between Olympic and Santa Cruz. Oaxaca could not have been derived from Santa Cruz except through Tree Line, however, because these two inversions are overlapping. But Oaxaca might have been derived from Olympic through still another hypothetical arrangement by double crossing over with Tree Line. This hypothetical arrangement is not the same as that by which Olympic might have been derived from Santa Cruz, avoiding Tree Line. But there is clearly no need to postulate such nonexistent arrangements, since all the facts can be simply accounted for by postulating the origin of both Oaxaca and Olympic from Tree Line, and the latter arrangement from Santa Cruz. It follows that, although included inversions do not in theory lend themselves to phylogenetic deductions, in

practice such deductions can safely be made if in nature a sufficient variety of gene arrangements are found which can be shaped into a consistent system.

Estes Park

Encountered in a sample from Estes Park, Colorado. This is another derivative of Tree Line, as is shown by the presence of a single rather short inversion in Estes Park / Tree Line heterozygotes (pl. 2). One of the breakage points lies in section 69B and the other in 79B, one disk removed from the dividing line of 79B and 74B in the Tree Line arrangement. This position of the distal break has been carefully checked in several preparations, since it is very close to the location of the distal break which transforms Santa Cruz into Tree Line. Estes Park / Tree Line overlaps the Tree Line / Santa Cruz inversion, rather than being included in the latter. At the same time, the proximal break in the Tree Line / Estes Park inversion is close to but not identical with the proximal break in Tree Line / Oaxaca; the two inversions are overlapping. Estes Park, however, like Oaxaca, is included in the Tree Line / Olympic inversion (fig. 3). Once more, we meet the possibility that Tree Line, together with a complementary arrangement which has never been encountered, may have been produced by double crossing over between Estes Park and Oaxaca chromosomes. But this hypothesis is unlikely for the reasons stated above in the discussion of the Oaxaca arrangement. The configurations Estes Park / Santa Cruz (pl. 2) and Estes Park / Oaxaca (pl. 3) have been examined; they show double overlapping inversions. The configurations Estes Park / Arrowhead and Estes Park / Pikes Peak are still more complex, almost to the degree of being unanalyzable; nevertheless, they occur in natural populations. The phylogeny of Estes Park, is:

Santa Cruz ⟵⟶ Tree Line ⟵⟶ Estes Park
Estes Park ⟵⟶ Tree Line ⟵⟶ Olympic
Estes Park ⟵⟶ Tree Line ⟵⟶ Oaxaca

Hidalgo

Observed in two chromosomes from Omitlan, Hidalgo, Mexico. According to the description and a drawing by Dobzhansky (1939a), Hidalgo / Tree Line heterozygotes have a single short inversion in the subterminal part of the chromosome. Hidalgo is derived from Tree Line by breaks in 72B and 77B, close to the dividing line with 78A. The Hidalgo inversion overlaps those which distinguish Tree Line from Santa Cruz and Tree Line from Estes Park, but is included in those which distinguish Tree Line from Olympic and from Oaxaca (cf. fig. 3). The simplest view regarding the phylogenetic relationships of Hidalgo is, therefore, that it is a Tree Line derivative, thus:

Santa Cruz ⟵⟶ Tree Line ⟵⟶ Hidalgo
Olympic ⟵⟶ Tree Line ⟵⟶ Hidalgo
Oaxaca ⟵⟶ Tree Line ⟵⟶ Hidalgo
Estes Park ⟵⟶ Tree Line ⟵⟶ Hidalgo

Mammoth

Encountered in a population sample from Mammoth Lakes, California, and since found in several localities near Death Valley, California. This gene arrangement has been seen only in heterozygotes with Standard and Arrowhead chromosomes, with which it forms a complex configuration having unpaired sections in the critical regions, a fact which makes these configurations difficult to analyze. According to Dobzhansky and Sturtevant (1938), Mammoth was derived from Santa Cruz by a single inversion with breaks in 75C and in 76B or 80A (cf. fig. 3). Although Mammoth / Santa Cruz heterozygotes have not been examined, this interpretation has been checked subsequent to publication of the paper just referred to. Assuming it to be valid, the inversion which transformed Santa Cruz into Mammoth overlaps those which distinguish Santa Cruz from Hypothetical and from Cuernavaca, and includes those which distinguish Santa Cruz from Chiricahua and from Tree Line. The phylogeny of Mammoth is probably thus:

$$\text{Hypothetical} \longleftrightarrow \text{Santa Cruz} \longleftrightarrow \text{Mammoth}$$

Cochise

This and the following two arrangements in *Drosophila pseudoobscura* have been seen in the offspring of a single fly each. They may represent either narrowly endemic forms which occur rarely in the populations of their given localities, or else spontaneous inversions which have arisen in the offspring of wild flies during their cultivation in the laboratory. Cochise was found in a sample from the Chiricahua Mountains, Cochise County, Arizona. It was called "Chiricahua II" in Dobzhansky and Sturtevant (1938) and in Dobzhansky (1937a, 1941b). It appears to have been derived from Arrowhead by inversion of sections 69, 70A, 76BA, and 75. The precise location of the breaks cannot be considered established.

Texas

Known from a single wild individual from Dilley, Texas. The heterozygotes examined had Texas and Pikes Peak chromosomes. They displayed a single fairly long inversion which was found in many cells. The slide was of good quality and the inversion was studied in detail, but, unfortunately, no drawing was made. Texas might have been derived from Pikes Peak by a single inversion, one break being located in 70C and the other just distal to the heavy doublet in 79B. The arrangement of sections in Texas is, consequently, as follows:

$$63, 64, 65\text{AB}, 75, 74\text{-}71, 70\text{DC} \mid 79\text{BA}, 78\text{-}76, 65\text{CD}, 66\text{-}69,$$
$$70\text{ABC} \mid 79\text{BCD}, 80, 81$$

The phylogeny of Texas may be considered established as follows:

$$\text{Standard} \longleftrightarrow \text{Pikes Peak} \longleftrightarrow \text{Texas}$$

San Jacinto

Discovered in a chromosome from Keen Camp, Mount San Jacinto, California. By a fortunate accident, this arrangement was found in a heterozygote with Chiricahua, from which it had arisen by a single inversion. Several good figures were examined. The San Jacinto / Chiricahua heterozygotes have a long inversion with breaks in 74B and 81B. The arrangement of sections in San Jacinto is, therefore, as follows:

63–67, 68AB, 79CD, 76A, 75, 74CB | 81BA, 80, 76BC, 77, 78A, 70, 69,
    68DC, 79BA, 78CB, 70D, 71–73, 74AB | 81BCD

The position of San Jacinto in the phylogenetic system is, therefore:

Santa Cruz ⟷ Chiricahua ⟷ San Jacinto

Finally, in a sample from Mount St. Helena, California, a chromosome was found which contained a gene arrangement not previously known. It occurred in combination with Standard and Arrowhead chromosomes and gave with them configurations which proved difficult to analyze. The strain with this gene arrangement was unfortunately lost before it could be re-examined.

Description of Gene Arrangements in the Third Chromosome of Drosophila persimilis

In *Drosophila persimilis,* seven gene arrangements are known in the third chromosome, in contrast with at least fifteen in *D. pseudoobscura.* Nevertheless, in view of the smaller area occupied by *D. persimilis,* its variability must be considered at least as great as that of *D. pseudoobscura.* Standard is the only gene arrangement common to both species. Descriptions of the other arrangements follow.

Klamath

Discovered in a sample taken near the mouth of Klamath River, California. It is the commonest arrangement in *D. persimilis,* except in the southern part of its area. It is derived from Standard by a single inversion with breaks in the distal part of 70C and in 77B (fig. 4). The description of these breaks and their location on the maps of Dobzhansky and Sturtevant (1938) are consequently inaccurate: the distal break is proximal, and not distal, to the heavy doublets in 77B, and the proximal break is close to the boundary of 70C and 70D, and not at the boundary of 70 and 71. The chromosome configuration in Standard / Klamath heterozygotes (pl. 4) greatly resembles that in Standard / Arrowhead (pl. 1). There is no doubt, however, that these inversions are different and overlapping (compare figs. 3 and 4). Klamath / Arrowhead heterozygotes, which can be obtained by artificial hybridization of *D. pseudoobscura* and *D. persimilis* but which are not known to occur in nature, have two small unpaired buckles in the distal part and close to the middle of the

third chromosome. The buckles contain parts of sections 70, 76, and 77. Sturtevant (1938) believes that crossing over between Klamath and Arrowhead chromosomes, or chromosomes as similar as these, might lead to formation of gametes with gene duplications and deficiencies, might lower the reproductive potential of the hybrids, and thus might become a starting point for the formation of reproductive isolating mechanisms that would transform races into species. There is no doubt that Klamath is related to Arrowhead not directly but only through Standard.
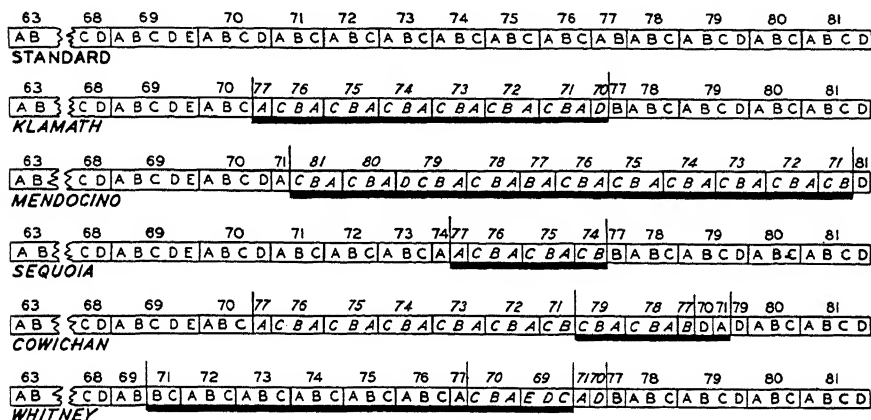
FIG. 4. The gene arrangements known in the third chromosome of *Drosophila persimilis*, in terms of the sections and subdivisions of the standard map.

Mendocino

Named Sequoia II in Dobzhansky and Sturtevant (1938) and Dobzhansky (1937a, 1941b), and Ukiah in Helfer (1941). Discovered in a sample from Ukiah, Mendocino County, California. The position of the breakage points and the descent relationships of this gene arrangement have been previously misinterpreted by Dobzhansky. Mendocino / Standard heterozygotes (pl. 4) have a single long inversion which includes approximately one-half the length of the chromosome. In figure 2 of Dobzhansky and Sturtevant (1938) this configuration is mislabeled "Sequoia II / Klamath." This error was evidently made because what in that figure was believed to be section 72 was in reality sections 76 and 77, and vice versa. The breakage points by which Mendocino can be derived from Standard are in 71A close to the dividing line with 71B, and in 81C close to the dividing line with 81D. The arrangement of sections in Mendocino is as shown in figure 4, and not as indicated in Dobzhansky and Sturtevant (1938) and in Helfer (1941). The inversion which transforms Standard into Mendocino overlaps that which relates Standard to Klamath (fig. 4). Mendocino / Klamath heterozygotes (pl. 4) have a double loop and usually unpaired distal ends of the third chromosome; this configuration is very characteristic and cannot readily be confused with any other recorded.

Mendocino is therefore related to Klamath through Standard, and not directly as was stated in the earlier paper. The phylogeny is:

Mendocino ⟷ Standard ⟷ Klamath

Sequoia

Discovered in a sample from Sequoia National Park, California, and named Sequoia I in Dobzhansky and Sturtevant (1938 and later work). Sequoia / Standard heterozygotes show a short inversion distal to the middle of the chromosome (pl. 4). The position of the breaks which transform Standard into Sequoia was also misinterpreted. Figure 2 in Dobzhansky and Sturtevant (1938) shows the configuration in a Sequoia / Klamath heterozygote, in which sections labeled 72, 73, 75, and 76 should be designated 74, 76, 73, and 72 respectively. There is, of course, a possibility· that the gene arrangement dealt with in the 1938 paper is not the same which was found and studied later from the same geographical area, but it is more likely that the old data were inaccurate. At any rate, the gene arrangement now being described is derived from Standard by breakages in 74B and at the dividing line between 77A and 77B (fig. 4). The inversion which distinguishes· Sequoia from Standard is included in those which distinguish Standard from Klamath and Mendocino. The distal breaks in Sequoia and Klamath are very close, but careful observation shows that a moderately heavy capsule and two faint dotted disks of 77B which are included in the Klamath are not included in the Mendocino. The phylogeny is probably:

Sequoia ⟷ Standard ⟷ Klamath
Sequoia ⟷ Standard ⟷ Mendocino

Whitney

Described by Dobzhansky and Queal (1938), from the eastern slope of Mount Whitney, Sierra Nevada, California. Klamath / Whitney heterozygotes have a single moderately short inversion. The Standard / Whitney configuration (pl. 4) is a double inversion; the shorter of the two loops, including section 70 and a part of 69, frequently fails to form, whereupon the chromosome straightens out but shows unpaired regions at its middle and in the subterminal part. Sequoia / Whitney heterozygotes have a somewhat more complex chromosome configuration which is puzzling at first sight but which is easily explained if one takes into account a triple inversion which is involved (pl. 4 and fig. 4). Whitney is derived from Klamath by breaks in 71A and 69C (fig. 4). Comparison of these breakage points with those in Klamath, Sequoia, and Mendocino (fig. 4) shows that all these inversions are overlapping. The descent relationships of Whitney are, therefore:

Whitney ⟷ Klamath ⟷ Standard

Cowichan

Found at Cowichan Lake, Vancouver Island, British Columbia. Cowichan / Klamath heterozygotes have a single short inversion in the subterminal region (pl. 4). Double inversions have been observed in Cowichan / Standard and Cowichan / Whitney heterozygotes, the latter of which is also shown in plate 4. The breakage points which transform Klamath into Cowichan are in sections 71A and at the boundary of 79C and D. These breakage points were correctly determined in Dobzhansky and Sturtevant (1938), but because the breaks in Klamath were reported incorrectly in that paper, the arrangement of sections in Cowichan was also incorrect. The proper arrangement of sections in Cowichan as well as in Klamath is shown in figure 4. Comparison of Cowichan with Whitney reveals that these inversions are apparently not overlapping; the distal break in Whitney coincides with the proximal break in Cowichan, or nearly so. Since division 71A contains faint disks, however, an exact coincidence of the breaks cannot be considered established. The inversions which relate Cowichan to Klamath and Klamath to Standard are clearly overlapping. The phylogeny is:

Cowichan ⟷ Klamath ⟷ Standard
Cowichan ⟷ Klamath ⟷ Whitney

Wawona

Described from a sample collected between Wawona and Coarse Gold, California. According to the description and a drawing published by Dobzhansky and Sturtevant (1938), Wawona is derived by a single inversion from Klamath and by two inversions from Standard. The breakage points have been determined to lie in 76A and 78A respectively. This would give the following order of sections in Wawona (corrected because of the mistakes previously made in determining the extent of the Klamath inversion):

63-70ABC, 77A, 76CBA | 78A, 77B, 70D, 71-75, 76A | 78ABC, 79-81

When the above-described Whitney gene arrangement was discovered, a striking similarity was observed between the Wawona / Standard configuration previously depicted by Dobzhansky and Sturtevant and the configurations observed in Whitney / Standard heterozygotes. It appeared possible that the Wawona / Standard configuration had been misinterpreted and that Wawona was in reality identical with Whitney. This conjecture seemed strengthened when succeeding population samples from various localities in northern California showed Whitney to be widespread and common, but no more chromosomes with the Wawona arrangement came into view. Yet in 1940 another chromosome identical with the old Wawona was found in a sample from Mariposa Grove, Yosemite National Park, a locality close by that in which Wawona was originally discovered. The configurations Wawona /

Standard and Wawona / Klamath were observed, but unfortunately no draw-
ings were made before the stock was discarded. It now seems clear that
Wawona and Whitney are two different and broadly overlapping inversions,
related to each other through Klamath. Wawona overlaps Cowichan but
Whitney does not. The astonishing similarity between Wawona / Standard
and Whitney / Standard configurations seems now to be due to the fact that,
when the small inversion loops fail to form, the chromosomes show unpaired
sections in about the same place. The two configurations are distinguishable
because sections 72 and 73, which serve as landmarks, are shifted in Wawona
toward the distal, and in Whitney toward the proximal, end of the chromosome.
The phylogeny of Wawona is:

<div align="center">

Wawona ⟷ Klamath ⟷ Standard
Wawona ⟷ Klamath ⟷ Whitney
Wawona ⟷ Klamath ⟷ Cowichan

</div>

In a sample from Orick, Humboldt County, California, a chromosome was
found which apparently differed from Klamath by a short inversion includ-
ing sections 71, 72, and 73. The stock was lost before a more careful study
was made. This gene arrangement is shown in figure 8 in Dobzhansky
(1941b) as "Humboldt," but it seems better to postpone its description until
more material is available.

<div align="center">

PHYLOGENY OF GENE ARRANGEMENTS AND DISTRIBUTION OF BREAKS IN THE
THIRD CHROMOSOME

</div>

A general scheme of descent relationships of the gene arrangements in the
third chromosome is given in figure 5. This scheme supersedes the similar
ones published earlier (Dobzhansky and Sturtevant, 1938; Dobzhansky,
1937a, 1941b). The two insufficiently studied arrangements (St. Helena in
Drosophila pseudoobscura, and Humboldt in *Drosophila persimilis*) are not
included. Some of the gene arrangements in the scheme are peripheral, that
is, related by a single inversion to only one or two other gene arrangements.
Others, namely Standard, Tree Line, Santa Cruz, and Klamath, occupy cen-
tral points in the scheme; each of them is related simply to four or more
arrangements. Standard, Tree Line, Santa Cruz, and Klamath are the heads
of "families" or "phylads" of gene arrangements, and it seems reasonable to
suppose that the gene arrangement phylogenetically ancestral to all others is
most likely to be found among them. Standard is not only the head of a large
phylad, but also the only arrangement which is known to occur in both
D. pseudoobscura and *D. persimilis*. It would therefore be reasonable to as-
sume that it existed in the common ancestor of these two species. An alter-
native, the Hypothetical, has not yet been found in nature, but it occupies
perhaps the most central position of all. Furthermore, it is remarkable in
another respect. As shown by Dobzhansky and Sturtevant (1938) and by

observations made since the publication of that paper, the gene arrangement of the third chromosome in *D. miranda* is more like that of Hypothetical than it is like any other arrangement in *D. pseudoobscura* or *D. persimilis*. Hypothetical or a closely similar arrangement might therefore have existed in the phyletic stock which gave rise to *D. miranda* on the one hand and to *D. pseudoobscura* and *D. persimilis* on the other. Finally, a third arrangement, Santa Cruz, occupies a position similar to that of Standard, if Hypothetical be considered the most central arrangement. That Santa 'Cruz is of great antiquity is suggested by its present geographic distribution and the dis-
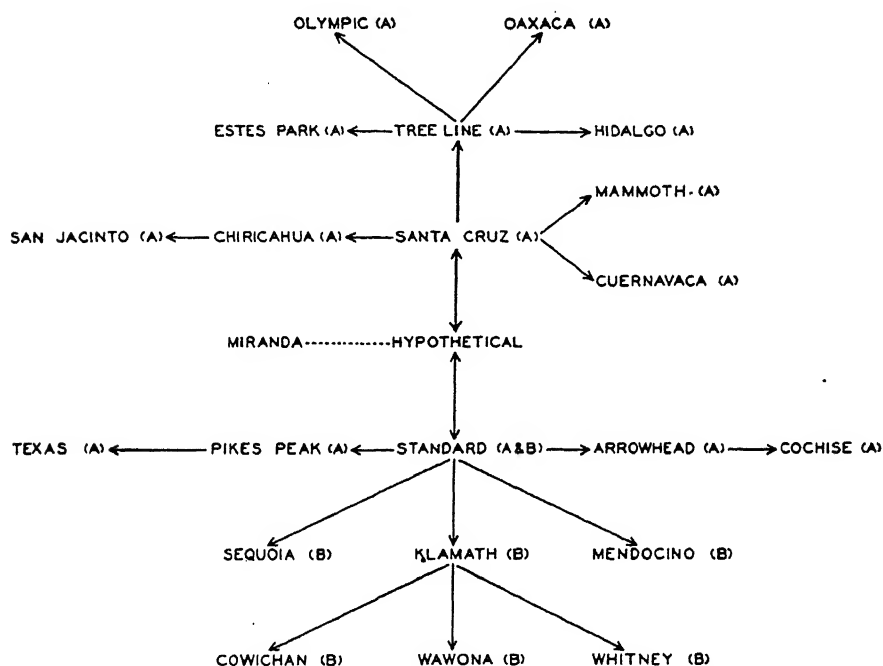
FIG. 5. The phylogeny of the gene arrangements in the third chromosome of *Drosophila pseudoobscura* (A) and *Drosophila persimilis* (B).

tributions of its derivatives (see below). Hypothetical, Standard, and Santa Cruz therefore seem to be the ancestral arrangements. This assumption is symbolized in figure 5 by the double-headed arrows which connect these arrangements, while other arrows are single-headed. If one of these arrangements be accepted as the starting point, the remainder of the scheme becomes fixed.

A summary of the data on the location of the breakage points observed in the naturally occurring gene arrangements is given below. If a break appears to coincide with the dividing line between two sections or divisions it is shown thus: 70C / D. This list supersedes that published by Helfer, 1941.

· 6

64C	. . . . Cuernavaca	75A	. . . . Olympic
65C	. . . . :. Pikes Peak	75C	. . . . Pikes Peak
68C	. . . . Santa Cruz, Tree Line?	76A	. . . . Hypothetical, Wawona
69B	. . . . Estes Park	76B	. . . . Arrowhead, Oaxaca
69C	. . . . Whitney	77A/B	. . . . . . Sequoia
69D	. . . . Oaxaca	77B	. . . . Klamath, Chiricahua,
70A	. . . . Cuernavaca		Hidalgo
70B	. . . . Arrowhead	78A	. . . . Wawona
70C	. . . . Texas	79B	. . . . Santa Cruz, Tree Line?,
70C/D	. . . . . . Klamath		Estes Park, Texas
70D	. . . . Chiricahua	79C/D	. . . . . . Cowichan
71A	. . . . Mendocino, Whitney,	79D/80A	. . . . Hypothetical
	Cowichan	80B	. . . . Olympic
72B	. . . . Hidalgo	81B	. . . . :. San Jacinto
74B	. . . . San Jacinto, Sequoia	81C	. . . . Mendocino
74B/C	. . . . . . Tree Line		

The distribution of the 38 breaks thus recorded is apparently not random. The heterochromatic region, which, according to Helfer (1941), is frequently involved in X-ray-induced chromosomal aberrations, is not disturbed by naturally occurring inversions. Nor is the distribution of breaks in the euchromatic part of the chromosome uniform. The two short sections 76 and 77 have eight breaks, the division 79B has three or four, and the sections from 63 to 68 inclusive, which constitute more than a third of the chromosome, have also three or four breaks. Although the total number of natural breaks is small, the deviation from randomness appears to be significant. Bauer, Demerec, and Kaufmann (1938) and Bauer (1939) in the chromosomes of *Drosophila melanogaster,* and Helfer (1941) in the third chromosome of *D. pseudoobscura,* found the incidence of X-ray breakage per unit length to increase slightly from the proximal to the distal end of the chromosome. The present data for natural breaks can be interpreted to show a similar distribution.

The sections in which the concentration of breaks is high do not display any visible peculiarity. The sections 76 and 77, for example, have many breaks and have many heavily stainable disks, but no breaks at all have been observed in 65A, 67, 72A, or 80C, which also abound in heavy disks. It may be pointed out that the chromosome sections which represent internal duplications (repeats) or interstitial heterochromatic regions show a high incidence of X-ray breakage (Kaufmann, 1940), but do not behave similarly with respect to natural breaks. Such sections are most frequent in the fourth and least frequent in the third chromosome of *D. pseudoobscura,* yet the gene arrangement is most variable in the latter and least variable in the former chromosome. In the third chromosome the only two certain repeats are in section 72A (see pairing configurations in Olympic / Tree Line and Chiricahua / Tree Line, plate 2, and Chiricahua / Pikes Peak, plate 3), and in section 73AB (see pairing configurations in Pikes Peak / Cuernavaca, plate 3, and Sequoia / Whitney, plate 4). No breaks have been observed in either section. If the observed

concentration of natural breaks in certain chromosome sections is not fortuitous, its cause is most likely the absence of deleterious position effects following breakage of these sections.

The distribution of breaks in the·chromosome can be considered from a still different angle. It is possible that the same chromosome section would show a different breakability if it lay in the distal part of the chromosome from what it would show if it had been transferred, by inversions, to the middle or to the proximal part. Or, it is possible that inversions established in nature may have a certain modal length, very long and very short inversions being avoided. Figures 3 and 4 suggest, however, that long (Pikes Peak, Cuernavaca), intermediate, and rather short (Sequoia, Cowichan) inversions all occur. Most inversions involve the distal half of the chromosome, but some (Mendocino) are subterminal; no definitely subbasal inversions are recorded, and their absence may be significant.

Gene Arrangement in Chromosomes Other than the Third

Second Chromosome

Tan (1935) has shown that *Drosophila pseudoobscura* differs from *D. persimilis* in a rather short inversion in the middle part of the second chromosome. Within either species the gene arrangement in the second chromosome is nearly constant. In *D. pseudoobscura* Tan (1935) found a subterminal inversion in a strain from the Santa Lucia Mountains, California, and Dobzhansky and Sturtevant (1938) observed a different inversion in three strains from New Mexico. In *D. persimilis* two more inversions have been found by Dobzhansky and Sturtevant (1938) in two samples from the Olympic Peninsula, Washington. Curiously enough, in all the material examined since 1938, including samples from New Mexico and from the Olympic Peninsula, no inversions of any kind have been detected in the second chromosomes.

Fourth Chromosome

The fourth chromosome is identical in the two species, the only variant observed being an inversion recorded in a strain from Cuernavaca, Mexico (Dobzhansky and Sturtevant, 1938).

X Chromosome

No variations in the gene arrangement in the left limb of the X chromosome have been observed, although, as shown by Tan (1935) and by Dobzhansky and Tan (1936), the XL's of the two species differ by an inverted section.

The right limb of the X chromosome (XR) is the only chromosome other than the third which shows an appreciable intraspecific variability. Three gene arrangements are known in this chromosome. One of them is normal for *D. pseudoobscura* and also occurs in "sex ratio" strains of *D. persimilis;* this is the standard arrangement. The second is found in all *D. persimilis*

strains free of the "sex ratio" condition. The third is encountered in "sex ratio" strains of ·D. pseudoobscura (Sturtevant and Dobzhansky, 1936a; Dobzhansky and Sturtevant, 1938; Dobzhansky, 1939c). Hybrids of D. pseudoobscura and D. persimilis, if they are free of "sex ratio," or D. persimilis individuals heterozygous for the "sex ratio" of that species, show a single inversion somewhat distal from the middle of the length of the chromosome (pl. 4). The gene arrangement characteristic for D. persimilis is derived from the Standard by breaks in sections 26 and 37.

Females of D. pseudoobscura heterozygous for the "sex ratio" have three independent inversions in the XR chromosome (pl. 4). One of these three inversions appears to be strictly terminal: the chromosome is broken in section 39, and the segment distal to the break, up to and including the standard free end, is inverted. The free end of the standard chromosome is very characteristic: the terminal disk is rather heavily staining, and usually consists of separate droplets. Complete pairing of this disk with its interstitially lying homologue has been seen in many cells of inversion heterozygotes. Individuals homozygous for the "sex ratio" X chromosome have also been examined; the free end of the XR in such individuals is distinctly different from normal. Those who doubt the existence of terminal inversions may, of course, postulate the existence of an invisible terminal disk ("telomere") which is not included in this inversion; all that is asserted here is that the inversion under consideration appears to be terminal, despite efforts to find the hypothetical invisible disk. The two other inversions are subbasal. The more proximal of them is relatively short and involves breaks in sections 22 and 24; the more distal one is long and involves breaks in 24 and 33. The uninverted piece which separates the two subbasal inversions is very short; it includes only 4 or 5 disks of section 24. Pairing of these disks in heterozygotes has been seen in only two cells among hundreds examined. The uninverted piece which separates the subbasal from the terminal inversions is long; it contains sections from 34 to 39 inclusive (pl. 4).

Numerous tests have shown that individuals which manifest the genetic effects of the "sex ratio" condition (unisexual or nearly unisexual progenies, cf. Sturtevant and Dobzhansky, 1936a) invariably have the correlated gene arrangements in the XR chromosomes, and vice versa. The nature of this association is unknown. Furthermore, it is remarkable that the three inversions which characterize the "sex ratio" separate very seldom, although crossing over should, at least occasionally, take place in the long uninverted segment lying between the subbasal and the terminal inversions. If the frequency of this crossing over is at all appreciable, an equilibrium would be expected in panmictic populations. If the initial frequency of the chromosomes with the three inversions is q, a proportion q^2 of the chromosomes should have the subbasal as well as the terminal inversions, $(1-q)^2$ should have neither, and $q(1-q)$ should have only the subbasal or only the terminal inversions, respectively. This is not observed. Although in some populations 15 per cent or more of the X chromosomes carry "sex ratio" (and, hence, the three inver-

sions), a chromosome with the subbasal inversions but lacking the terminal one has never been found. Only two chromosomes with the terminal but without the subbasal inversions have been recorded. One of these has been tested genetically by Miss A. M. Holz, and found not to produce the "sex ratio" effect. The problem is further complicated by the observation that the "sex ratio" in *Drosophila azteca* is likewise associated with three independent inversions in the X chromosome, and here, again, only chromosomes with three and with no inversions occur in natural populations. As a working hypothesis, one may suppose that the crossovers either are rarely produced, or else are eliminated in nature because of a lowered viability.

PRIMARY DATA FOR THE GENE ARRANGEMENTS IN THE THIRD CHROMOSOME

The primary data on the gene arrangements in the third chromosome from different geographic regions are summarized in tables 1 and 2 for *Drosophila pseudoobscura* and in table 3 for *D. persimilis*. The figures in these tables show the numbers of chromosomes which carry the respective gene arrangements found in the populations sampled. These are the primary, but not the raw, data. The raw data consist of records which show the gene arrangements in the two chromosomes of each larva examined under the microscope; from such observations the chromosomes probably present in the wild progenitors of the larva in question have been deduced with the aid of the reasoning outlined in the section on "Material and Technique." The raw data are too extensive to be published; we shall refer to them, however, in discussing the relative frequencies of homo- and heterozygotes for various gene arrangements in natural populations.

The localities in tables 1 to 3 are grouped roughly from north to south and from west to east. The locality names given are those of the towns, mountain ranges, valleys, or rivers nearest to the respective stations at which samples were obtained. Such locality designations are of necessity inexact; they show neither the precise point on the map from which the flies came, nor the environment (vegetation, etc.) and the dates of collecting. This information being of some importance, it is given below in the briefest possible fashion in the form of a list of collecting localities. In this list, the names of the localities as given in tables 1 to 3 are shown in *italics*. The names of some collectors are abbreviated: Th. Dobzhansky, D; C. Epling, E; and J. T. Patterson or his collaborators, P. With few exceptions the early collecting (on which the paper of Dobzhansky and Sturtevant, 1938, was based) is included neither in the tables nor in the list of localities, because this early material was examined for the gene arrangements only after the strains had been kept in the laboratory for several generations. The resulting data were therefore qualitatively but not quantitatively valid. They are included on the maps (figs. 6–9). The approximate elevations of certain localities are given where they seem significant.

BRITISH COLUMBIA. Between Laidlaw and Flood, near *Hope,* June 1940, W. Hovanitz. 10 miles east of *Princeton,* June 1940, W. Hovanitz.

WASHINGTON. *Friday Harbor,* July 1940, H. K. Fink. Sammamish Lake near *Seattle,* June 1940, W. Hovanitz. *Seattle,* August 1940, R. D. Boche. Junction of Cold Creek and *Methow* River, June 1940, W. Hovanitz. 8 miles southwest of South Bend on *Willapa Bay,* June 1940, W. Hovanitz.

OREGON. *Cape Perpetua,* 3 miles south of Yachats, June 1940, W. Hovanitz. *Selma* River near Kerby, oak and ponderosa pine wood, July 1940, D and E. 3 miles south of Dale, *Whitman National Forest,* June 1940, W. Hovanitz. Service Creek near *Spray,* August 1940, J. E. Cushing.

CALIFORNIA, NORTHERN COAST RANGES. *Coffee Creek,* oak and pine forest, July 1940, D and E. Prairie Creek Redwood Park near *Orick,* July 1940, D and E. Humboldt Redwood Park near *Weott,* July 1940, D and E. Boundary of Mendocino and Tehama Counties near Mount *Yollo Bolly,* two samples, at about 6000 feet in white fir, and at 3000 feet in pine, oak, and madroño belt, July 1940, D and E. Between *Mendocino* and Melbourne, *Pinus muricata* forest, July 1940, D and E. *Ukiah, Hopland, Guerneville, Forestville, Sebastopol,* and *Cotati,* April 1938 and October 1937, A. H. Sturtevant. Between Calistoga and Middletown, slopes of *Mount St. Helena,* mixed forest, July 1940, D and E.

NORTHEASTERN CALIFORNIA AND SIERRA NEVADA. Near Hackamore, *Alturas* County, June 1940, W. Hovanitz. Between Butte Meadows and Childs Meadows, *Deer Creek,* 4500 feet, Lassen National Forest, July 1940, D and E. *Lake Tahoe,* September 1940, G. Mainland. Between Placerville and Pacific near *Camino,* 4000 feet, July 1940, D and E. *Mariposa Grove,* Yosemite National Park, sequoia grove, July 1940, D and E. *Stony Creek,* between Grant and Sequoia National Parks, July 1940, W. Hovanitz. *Atwell Mill,* sequoia forest, August 1940, D. *Mineral King,* 8000 feet, August 1940, D. Upper *Funston Meadow,* Sequoia National Park, 6700 feet, ponderosa pine near a stream, August 1940, D. *Rattlesnake Meadow,* Sequoia National Park, 8000 feet, aspen and fir, August 1940, D. *Lone Pine Canyon,* 7500 feet, collections in July 1937, D; July 1938, P. C. Koller and D; June 1940, D; this locality is referred to by Dobzhansky and Queal (1938) and by Koller (1939) as "Whitney."

CALIFORNIA, SOUTHERN COAST RANGES. Between *Monterey* and Carmel, August 1940, D and E. *Santa Lucia Mountains,* between Jolon and San Simeon, oak-madroño woodland, May 1940, E. *San Rafael Mountains,* Davy Brown Camp, oak-pine woodland, April 1940, E. *Santa Barbara* and environs: *Tucker's Grove, Moore's Ranch, Mission Canyon, Lauro Canyon, Swamp on U. S. 101,* September 1940, G. Mainland.

CALIFORNIA, CHANNEL ISLANDS. *Santa Rosa* Island, oak and pine grove near top of central mountain peak, October 1939, D and E; June 1941, E. *Santa Cruz* Island, wooded canyon on north coast and among pines on slope of Diablo Peak, May 1936, A. H. Sturtevant, J. F. Bonner, and D; on *Pinus muricata* near sheep ranch, May 1940, W. Hovanitz.

CALIFORNIA, SOUTHERN SECTION. *Santa Monica,* oak woodland, April 1940, E. Arroyo Seco near *Pasadena,* 3000 feet, oak-*Pseudotsuga* woodland, July 1939, W. Hovanitz. Camp Rincon in *San Gabriel* canyon, November 1936 and April 1937, A. H. Sturtevant and W. P. Spencer. *Keen Camp,* Mount San Jacinto, 4500 feet, *Piñon Flat,* 4000 feet, and *Andreas Canyon,* 800 feet: many samples taken repeatedly in the same localities from 1939 to 1942, W. Hovanitz, E. Held, A. Sokoloff, D, E,

and others (these samples will be described in detail elsewhere, only a summary being given in table 1). *Borego* Valley, desert vegetation, April 1941, E. *Banner* and *Julian,* see Dobzhansky and Sturtevant (1938); *Joshua Tree National Monument,* Jaeger's Cove, April 1941, E. *Chuckwalla* Mountains, desert vegetation, April 1941, E. Cottonwood Spring, *Pinto Basin,* desert spring vegetation, March and May 1939, A. H. Sturtevant and D. *Bagdad,* Mojave Desert, desert vegetation, April 1941, E.

BAJA CALIFORNIA. *Santo Tomas* and *Guadalupe,* two samples combined, April 1936, A. H. Sturtevant. Near *San Antonio Mesa,* pine and cypress woodland, March 1940, E. *Cedros Island,* combined samples from *Pinus muricata* groves at 1700 feet and from desert zone at a lower level, March 1939, A. L. Haines and George Hale.

CALIFORNIA AND NEVADA, DEATH VALLEY REGION. This region and the collections made in it have been described by Dobzhansky and Queal (1938) and Koller (1939). The collecting stations referred to in Dobzhansky and Queal's paper as "Panamint" (Telescope) correspond in part to that named "Wildrose" in Koller's paper. In 1939 four collecting stations, referred to as Wildrose A, B, C, and D, were established: Wildrose A corresponds to Koller's "Wildrose"; Wildrose A and Wildrose B combined, with the intervening territory, correspond to Dobzhansky's (1937b) "Panamint"; Wildrose C and D are at Piñon Mesa, about 3 miles from Wildrose A and B. Elevation of Wildrose A and B about 7900–8000 feet, not 8300 feet as stated in Dobzhansky and Queal's paper.

UTAH. Wasatch Mountains near *Salt Lake City,* August 1940, F. Bonner; August 1941, D. *Uinta Mountains,* near Soapstone Cabin, August 1941, D. *Bryce National Park,* ponderosa pine forest, June 1940, D.

ARIZONA. *Kaibab National Forest,* near Kaibab Lodge, 8900 feet, aspen and fir forest, June 1940, D. *Cape Royal,* Grand Canyon National Park, *Pinus edulis,* June 1940, D. 7 miles east of *Flagstaff,* ponderosa pine forest, June 1940, D. *Black Mesa* near Summit Lake, *Pinus edulis* grove, June 1940, D. 5 miles south of *Prescott,* ponderosa pine and oak forest, June 1940, D. *Chiricahua Mountains: Cave Creek, National Monument, Rustler Park,* September 1940 and August 1941, P. *Williams Ranch,* San Bernardino, August 1941, P. *Ashton Draw,* San Bernardino, August 1941, P. *Huachuca Mountains,* summit and Ramsey Canyon, August 1941, P; pine and oak forest, September 1940, E. *Tucson,* April 1941, E. *Sonoita,* desert vegetation, April 1941, E. *Castle Dome,* April 1941, E. Near *Yuma,* desert vegetation, April 1941, E.

WYOMING. *Jackson Hole,* August 1940, A. H. Sturtevant.

COLORADO. Muggins Gulch near *Estes Park,* August 1941, D. Mountains near *Boulder,* September 1940, J. Ewan. *Mount Campbell,* August 1941, D. North Cheyenne Canyon near *Pikes Peak,* August 1941, D. *Mesa Verde* National Park, July 1940, W. P. Spencer.

NEW MEXICO. *Raton Mesa,* July 1940, W. P. Spencer. Desert near *Cliff,* September 1940, G. Mainland. Desert in *Grant County,* September 1940, G. Mainland. *Silver City,* September 1940, G. Mainland. *Gila* River, October 1941, P. *Radium Springs,* August 1941, P. 2 miles north of *Las Cruces,* August 1941, P. *Capitan,* October 1941, P. *Hondo,* October 1941, P.

NEBRASKA. *Gibbon,* A. H. Sturtevant.

TEXAS. All the samples from this state were collected by J. T. Patterson and his

collaborators, from 1939 to 1941. At *Aldrich* Place, near Austin, Patterson has collected repeatedly during the breeding season.

MEXICO, NUEVO LEÓN. *San Josecito,* April 1941, Bob Camp.

MEXICO, CHIHUAHUA. About 40 miles north of *Chihuahua City,* cactus patch, October 1942, G. Mainland. Gage Ranch, *Santa Clara Mountains,* October 1942, G. Mainland.

MEXICO, SONORA. *Magdalena,* August 1941, P.

All other Mexican collections were made by Dobzhansky, and described in Dobzhansky, 1939*a.*

TABLE 1

GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
British Columbia									
Hope	5	6	...	...	3	...	...	...	14
Princeton	6	8	1	...	...	1	...	...	16
Washington									
Friday Harbor	15	3	2	...	1	6	1	...	28
Seattle	23	5	...	...	13	3	...	...	44
Methow	52	47	...	...	1	...	...	...	100
Willapa Bay	8	1	2	...	3	...	...	...	14
Oregon									
Cape Perpetua	2	...	...	...	...	...	...	...	2
Selma	12	34	...	1	12	5	...	...	64
Whitman Nat. Forest.	6	10	...	...	2	...	2	...	20
Spray	22	50	4	...	10	2	...	...	88
California, northern Coast Ranges									
Coffee Creek	14	44	...	...	1	2	...	...	61
Weott	2	2	...	...	...	...	...	...	4
Yollo Bolly, upper	3	6	...	...	...	2	1	...	12
Yollo Bolly, lower	8	18	...	2	2	4	2	...	36
Mendocino	37	25	...	1	7	...	...	...	70
Ukiah	5	5	...	...	...	...	...	...	10
Hopland	7	6	1	2	...	...	...	...	16
Guerneville	6	1	...	6	...	1	...	...	14
Forestville	17	4	...	7	...	2	...	...	30
Sebastopol, 1937	2	4	2	4	...	...	...	...	12
Sebastopol, 1938	6	1	...	10	...	1	...	...	18
Cotati	11	2	...	8	...	1	...	...	22
Mt. St. Helena	38	22	...	13	12	19	3	1 *	108

* Undefined, perhaps new.

(*Continued on following page*)

TABLE 1—*Continued*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
Northeastern California and Sierra Nevada									
Alturas ...	...	11	...	...	...	1	...	...	12
Deer Creek	32	68	...	1	4	4	3	...	112
Lake Tahoe	4	9	...	...	4	2	5	...	24
Camino	29	29	...	20	7	15	8	...	108
Mariposa Grove	27	28	...	2	7	7	1	...	72
Stony Creek	1	1	...	...	...	...	...	...	2
Atwell Mill	31	28	1	1	3	3	1	...	68
Mineral King	16	15	...	...	2	2	1	...	36
Rattlesnake Meadow	3	7	...	...	2	2	2	...	16
Funston Meadow	5	6	...	1	4	2	2	...	20
Lone Pine Canyon,1937	10	32	...	...	4	...	...	...	46
Lone Pine Canyon, 1938 †	20	53	...	...	17	3	1	...	94
Lone Pine Canyon,1940	10	32	...	...	7	5	1	...	55
California, southern Coast Ranges									
Monterey	35	8	...	13	5	...	3	...	64
Santa Lucia Mts.	53	21	...	14	13	2	1	...	104
San Rafael Mts.	48	20	...	5	12	5	2	...	92
Santa Barbara	32	12	...	7	12	7	...	...	70
Tucker's Grove	6	3	...	1	...	...	...	...	10
Moore's Ranch	55	17	...	10	17	3	...	...	102
Mission Canyon	46	28	...	6	22	12	...	...	114
Lauro Canyon	19	8	...	5	7	5	...	...	44
Swamp on U. S. 101	2	3	...	...	1	...	...	...	6
California, Channel Islands									
Santa Rosa, 1939	4	2	...	13	3	2	...	...	24
Santa Rosa, 1941	31	5	...	12	7	1	...	...	56
Santa Cruz, 1936	23	7	...	12	...	...	...	...	42
Santa Cruz, 1940	31	13	...	23	5	...	...	...	72
California, southern section									
Santa Monica	13	9	...	1	7	4	...	...	34
Pasadena	116	23	...	4	20	5	...	...	168

† Published in Koller, 1939.

TABLE 1—*Continued*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
San Gabriel, 1936	8	15	...	...	22	9	...	...	54
San Gabriel, 1937	27	13	...	...	5	2	...	...	47
Keen Camp A	487	373	...	3	539	52	...	...	1454
Keen Camp B	261	206	...	...	336	32	...	...	835
Keen Camp C	204	212	...	...	342	26	...	...	784
Keen Camp D	333	308	...	3	428	47	...	1**	1120
Keen Camp E	284	226	...	1	406	31	...	...	948
Piñon Flat A	866	528	...	11	549	85	...	...	2039
Piñon Flat B	371	271	...	6	298	36	...	...	982
Andreas Canyon A	1432	586	...	11	323	70	...	...	2422
Andreas Canyon B	592	269	...	3	186	22	...	...	1072
Borego	25	15	...	...	2	...	...	...	42
Banner	24	11	...	1	6	...	...	...	42
Julian	22	14	...	2	10	...	...	...	48
Joshua Tree Nat. Monument	13	9	...	...	2	...	...	...	24
Chuckwalla	4	2	...	...	...	...	...	...	6
Pinto Basin	15	7	...	1	5	4	...	...	32
Bagdad	1	7	...	...	...	...	...	...	8
Baja California									
Santo Tomas and Guadalupe	19	9	...	3	1	...	...	...	32
San Antonio Mesa	42	17	...	...	13	...	...	...	72
Cedros Island	14	8	...	4	...	...	...	...	26
California and Nevada, Death Valley region									
Panamint Mts. (excluding Wildrose)†	349	367	...	...	177	23	...	...	916
Wildrose A and B, 1937	31	151	...	...	42	...	...	...	224
Wildrose A, May 1938 †	53	59	...	3	39	1	...	1 ‡	156
Wildrose A, October 1938	23	31	...	2	14	4	...	...	74
Wildrose A, 1939	67	87	...	1	29	6	...	...	190
Wildrose A, 1940	26	46	...	...	28	6	...	...	106
Wildrose B, 1939	58	97	...	...	26	9	...	...	190
Wildrose B, 1940	27	56	...	...	16	...	...	1 ‡	100

** A new gene arrangement.
† Published in Koller, 1939.
‡ Mammoth gene arrangement.

TABLE 1—*Continued*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
Wildrose C, 1939	37	49	...	...	13	1	..	...	100
Wildrose C, 1940	19	21	...	...	12	1	...	1 ‡	54
Wildrose D, 1939	52	34	...	...	12	2	...	...	100
Wildrose D, 1940	39	37	...	...	20	4	..	...	100
Magruder, Coso, Cottonwood, and Avawatz Mts. §	189	555	...	...	92	...	..	2 ‡	838
Grapevine, Kingston, Charleston, and Sheep Mts. §	184	603	...	...	107	...	...	..	894
Argus Range	4	16	...	...	4	...	...	...	24
Toyabe Range	1	13	...	...	2	...	...	...	16
Providence Mts. §	24	246	...	...	30	...	...	..	300
Utah									
Salt Lake City, 1940..		4	...	...	...	...	...	...	4
Salt Lake City, 1941..		6	...	...	...	...	...	...	6
Uinta Mts.		19	1	...	...	...	...	...	20
Bryce Nat. Park......	2	96	...	...	2	...	...	...	100
Arizona									
Kaibab Nat. Forest....	...	96	...	...	4	...	...	.	100
Cape Royal	1	98	...	...	1	...	.	..	100
Flagstaff	1	97	1	...	1	...	.	...	100
Black Mesa	3	64	1	...	...	...	.	...	68
Prescott	11	79	1	..	9	...	...	.	100
Chiricahua Mts., Cave Creek, 1940	1	18	...	...	1	..	.	.	20
Chiricahua Mts., Cave Creek, 1941		44	2	...	1	1	.	.	48
Chiricahua Mts., Cave Creek Camp	...	10	1	...	1	.		.	12
Chiricahua Mts., mouth of Cave Creek		22	2	...	2	.		.	26
Chiricahua Mts., Nat. Monument		19	1	...	2	..		.	22
Chiricahua Mts., Rustler Park		17	.		1			.	18
Williams Ranch		30	2		4			.	36

‡ Mammoth gene arrangement.
§ Published in Dobzhansky and Queal, 1938.

TABLE 1—*Continued*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
Ashton Draw	...	10	...	...	...	...	...	...	10
Huachuca Mts.	...	18	1	...	9	...	...	...	28
Huachuca Mts., Ramsey Canyon	1	8	1		...	...	...	...	10
Huachuca Mts., summit	...	27	3	...	4	...	...	...	34
Tucson	1	3	...	...	4	...	...	...	8
Sonoita	3	25	...	...	14	...	...	...	42
Castle Dome	2	4	...	...	2	...	...	...	8
Yuma	6	25	...	...	1	...	...	...	32
· Wyoming									
Jackson Hole	...	2	...	...	...	...	...	...	2
Colorado									
Estes Park	3	11	37	...	...	5	...	8 *	64
Boulder	...	1	1	...	...	...	...	...	2
Mt. Campbell	3	33	19	...	...	...	3	4 *	62
Pikes Peak	...	4	4	...	...	...	...	...	8
Mesa Verde	...	100	...	...	...	...	...	...	100
New Mexico									
Raton Mesa	...	78	20	...	1	1	...	...	100
Cliff	...	22	2	...	...	...	...	...	24
Grant County	...	29	1	...	...	...	...	...	30
Silver City	...	68	1	...	...	1	...	...	70
Gila	...	17	3	...	4	...	...	...	24
Radium Springs	1	55	8	...	...	...	...	...	64
Las Cruces	...	42	4	...	3	1	...	...	50
Capitan	...	22	16	...	2	...	...	...	40
Hondo	...	58	34	...	8	2	...	...	102
Nebraska									
Gibbon	...	1	1	...	...	...	...	...	2
Texas, Trans-Pecos area									
El Paso	...	2	...	...	...	...	...	...	2
Marfa	2	48	73	...	5	7	...	1 *	136
Fort Davis	...	1	3	...	...	...	...	...	4
Lower Limpia Canyon	...	4	14	...	...	...	...	...	18

* Estes Park gene arrangement.

TABLE 1—*Continued*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
Middle Limpia Canyon ...		2	6	...	...	...	...	...	8
Davis Mts., State Park. ...		1	7	...	...	...	...	...	8
MacDonald Observatory ...		...	4	...	...	.. .	. ...	...	4
Chisos Mts., Oak Creek ...		...	32	...	...	...	...	...	32
Texas, Plains area									
La Mesa		13	16	...	...	...	...	1 *	30
Ozona		10	42	...	...	2	...	...	54
Throckmorton		1	7	...	...	...	...	...	8
Texas, north-central section									
Brownwood		6	6	...	...	...	...	...	12
Wichita Falls		3	1	...	...	...	...	...	4
Fort Worth		7	7	...	...	1	1	...	16
Plano		1	1	...	...	...	...	...	2
Arlington		3	8	...	...	1	...	...	12
Aldrich, March 16, 1939 ...		7	36	...	...	1	...	...	44
Aldrich, March 22, 1939 ...		24	71	...	...	8	...	1 *	104
Aldrich, March 26, 1939 ...		1	15	...	...	...	...	...	16
Aldrich, April 2, 1939. ...		3	13	...	...	1	...	1 *	18
Aldrich, April 3, 1939. ...		5	36	...	...	4	...	1 *	46
Aldrich, April 5, 1939. ...		8	33	...	...	2	...	1 *	44
Aldrich, April 19, 1939 ...		3	20	...	...	1	...	...	24
Aldrich, April 21, 1939 ...		17	42	...	...	2	...	1 *	62
Aldrich, April 23, 1939 ...		17	44	...	...	5	1	1 *	68
Aldrich, April 25, 1939 ...		1	22	...	...	1	...	...	24
Aldrich, April 27, 1939 ...		5	23	...	...	...	...	...	28
Aldrich, May 1939.... ...		10	74	...	...	4	...	1 *	89
Aldrich, November 1939 ...		2	18	...	...	2	...	...	22
Aldrich, December 1939 ...		1	13	...	...	2	...	...	16
Aldrich, January 12, 1940		...	12	...	...	2	...	...	14
Aldrich, March 6, 1940 ...		9	38	...	...	3	4	...	54
Aldrich, March 10, 1940 ...		26	60	...	...	5	3	...	94
Aldrich, March 15, 1940 ..		30	40	...	...	3	1	...	74
Aldrich, March 23, 1940 ..		17	55	. ..	...	6	2	...	80
Aldrich, March 28, 1940 ...		15	42	...	...	7	...	...	64
Aldrich, April 1, 1940		8	25	...	...	3	2	...	38
Aldrich, April 11, 1940. ...		16	29	...	...	2	1	...	48
Aldrich, April 15, 1940. ...		2	13	...	...	...	...	1 *	16
Aldrich, April 22, 1940. ...		19	54	...	...	6	...	1 *	80

* Estes Park gene arrangement.

TABLE 1—*Continued*

Locality	Standard	Arrowhead	Pikes Peak	Santa Cruz	Chiricahua	Tree Line	Olympic	Others	No. chromosomes examined
Aldrich, April 29, 1940. ...	9	30	...	...	6	1	...	46
Aldrich, May 1940.... ...	7	27	...	...	2	2	...	38
Aldrich, April 1941.... ...	1	23	...	...	2	2	...	28
Texas, south-central section									
San Antonio	1	7	...	...	2	...	...	10
Uvalde	17	122	...	...	16	3	...	158
Quemado	1	2	...	...	2	1	...	6
Eagle Pass	2	35	...	...	2	...	1 *	40
Carrizo Springs	4	6	...	...	1	4	1 *	16
Catarina	1	19	...	...	5	3	1	29
Dilley 1	22	84	...	...	19	5	1 *	132
Texas, Valley section									
Alice	1	15	...	...	3	1	...	20
Falfurrias	...	8	...	...	2	...	...	10
Three Rivers	1	19	...	...	5	3	...	28
Mexico, Nuevo León									
San Josecito	1	3	1	...	12	16	1 *	34
Mexico, Chihuahua									
Chihuahua City	18	72	7	144	3	2	...	246
Santa Clara Mts....... ...	3	6	...	30	...	1	...	40
Mexico, Sonora									
Magdalena	2	1	...	1	...	...	...	4

* Estes Park gene arrangement.

A general summary of the distributions of the gene arrangements recorded in tables 1 to 3 is presented in the form of maps in figures 6 to 9. The gene arrangements which have been found in a single chromosome each (Cochise, Texas, San Jacinto, and Humboldt) are not included. In *D. pseudoobscura,* the Standard phylad of gene arrangements is common in the United States and in British Columbia (fig. 6). Standard itself, the head of the phylad, is commonest along the Pacific coast, from British Columbia to Baja California, but it occurs sporadically as far inland as the Rocky Mountains and Texas. Its derivative Arrowhead appears to be omnipresent from British Columbia to the Mexican border, and is also found in the four samples available from northern Mexico (Nuevo León, Chihuahua, and Sonora). Populations of

TABLE 2

Gene arrangements in the third chromosome of *Drosophila pseudoobscura* in southern Mexican and Guatemalan populations

Locality	Santa Cruz	Cuernavaca	Chiricahua	Tree Line	Olympic	Estes Park	Oaxaca	Others	No. chromosomes examined
Southern Mexico									
Pachuca, Hidalgo	45	...		27	14	2	...	2 *	90
Tehuacan, Puebla	11	.·.		2	...	3	...	...	16
Orizaba, Vera Cruz... ...	27	...		5	...	4	4	...	40
Puebla, Puebla	13	1		11	...	5	...	...	30
Amecameca, Mexico ..	1	17	2	11	...	19	...	...	50
Cuernavaca, Morelos		4	...	...	...	...	...	...	4
Zitacuaro, Michoacan .	2	9	...	4	...	...	1	...	16
Morelia, Michoacan ..	2	...	...	4	...	...	...	...	6
Patzcuaro, Michoacan.	18	8	...	2	2	...	...	2 †	32
Guatemala									
Quezaltenango	35	6	...	15	...	...	...	...	56
Momostenango	1	...	...	1	...	...	...	...	2
Totonicapan	9	1	...	3	...	...	1	...	14
Huehuetenango	5	...	...	1	...	...	...	...	6
Sacapulas	4	...	...	...	...	...	...	...	4
Atitlan	2	1	...	1	...	...	...	...	4

* Hidalgo gene arrangement.
† Pikes Peak gene arrangement.

northern New Mexico and southern Colorado seem to be homozygous for Arrowhead. Pikes Peak, the other derivative of Standard, is commonest in the eastern part of the distribution area, from the Rocky Mountains of Colorado to Nebraska and Texas. It will probably be found also in the northern part of the Rocky Mountain System, which remains an inadequately known region. Pikes Peak is also recorded along the Pacific coast from British Columbia south to San Francisco Bay, but in that region it is rare. From the southern Rockies it diffuses westward into Arizona, Nuevo León, Chihuahua, Sonora, and even as far as Michoacan, Mexico. It is definitely absent only in southern California. The Standard phylad as a whole is rare or absent in southern Mexico and in Guatemala.

The Santa Cruz phylad (fig. 7) centers very definitely in Mexico and Guatemala and along the Pacific coast of the United States. The head of the phylad, Santa Cruz, occurs along the coast from northern California to Baja California, in the Sierra Nevada, and from Chihuahua and Nuevo León to Guatemala. The Pacific coast of northern Mexico being unknown, it is difficult to tell whether Santa Cruz really has the disjunct distribution which it appears to have. If it is absent from the Sierra Madre Occidental of Mexico, a gap sepa-

TABLE 3

G<small>ENE ARRANGEMENTS IN THE THIRD</small> CHROMOSOME OF *Drosophila persimilis*

Locality	Standard	Sequoia	Mendocino	Klamath	Cowichan	Whitney	Wawona	No. chromosomes examined
British Columbia								
Hope	...	...	...	18	1	1	...	20
Princeton	...	...	...	4	...	...	...	4
Washington								
Seattle	...	...	...	20	...	...	...	20
Willapa Bay	...	...	...	85	1	...	...	86
Oregon								
Cape Perpetua	...	...	4	96	2	...	...	102
Selma	2	...	5	43	...	...	...	50
Whitman Nat. Forest	1	...	...	6	...	1	...	8
California, Coast Ranges								
Orick	1	1	57	46	...	1	...	106
Coffee Creek	7	...	3	26	1	1	...	38
Weott	7	...	17	34	...	...	...	58
Yollo Bolly, upper	7	...	6	25	...	...	...	38
Yollo Bolly, lower	8	...	4	18	...	4	...	34
Mendocino	8	1	78	24	...	1	...	112
Ukiah	6	...	3	17	...	...	...	26
Hopland	1	...	...	1	...	...	...	2
Forestville	...	...	...	2	...	...	...	2
Mt. St. Helena	2	...	2	2	...	...	...	6
Monterey	...	...	4	...	...	...	...	4
Northeastern California and Sierra Nevada								
Deer Creek	1	1	...	8	...	4	...	14
Mariposa Grove	3	...	...	1	...	4	2	10
Stony Creek	16	...	...	1	...	5	...	22
Atwell Mill	23	...	1	...	...	12	...	36
Mineral King	13	1	...	...	...	28	...	42
Funston Meadow	33	1	1	2	...	23	...	60
Rattlesnake Meadow	14	2	...	1	...	47	...	64
Lone Pine Canyon, 1937	15	...	...	1	...	58	...	74
Lone Pine Canyon, 1938 *	18	...	...	5	...	47	...	70
Lone Pine Canyon, 1940	8	1	...	4	...	39	...	52
California, Death Valley region								
Coso Range	6	...	...	...	...	14	...	20

* Published in Koller, 1939.

rates the Santa Cruz localities in Baja California from those in Chihuahua and in Michoacan. It is possible, however, that Santa Cruz will be found along the peninsula of Baja California and in the Mexican states of Sinaloa and Nayarit, in which case the gap would be reduced to the width of the Gulf of

FIG. 6. Geographic distribution of the Standard phylad of gene arrangements in the third chromosome of *Drosophila pseudoobscura*.

California. Among the derivatives of Santa Cruz, Chiricahua and Cuernavaca are the commonest. Chiricahua centers on the Pacific coast of the United States and in northern Mexico (Chihuahua), but it diffuses much farther northward (as far as British Columbia) and eastward (as far as western Texas) than the Santa Cruz itself. Chiricahua is found sporadically up to and including southern Mexico (the state of Oaxaca), but is apparently absent from

7

Guatemala, thus not crossing the Isthmus of Tehuantepec. Its distribution is certainly not disjunct, since it is very common in northern Mexico. In fact, it is the commonest gene arrangement in northern Mexico (Chihuahua); it is fairly common in southern Arizona and in southern California. Cuernavaca is endemic in southern Mexico and Guatemala, being the commonest gene
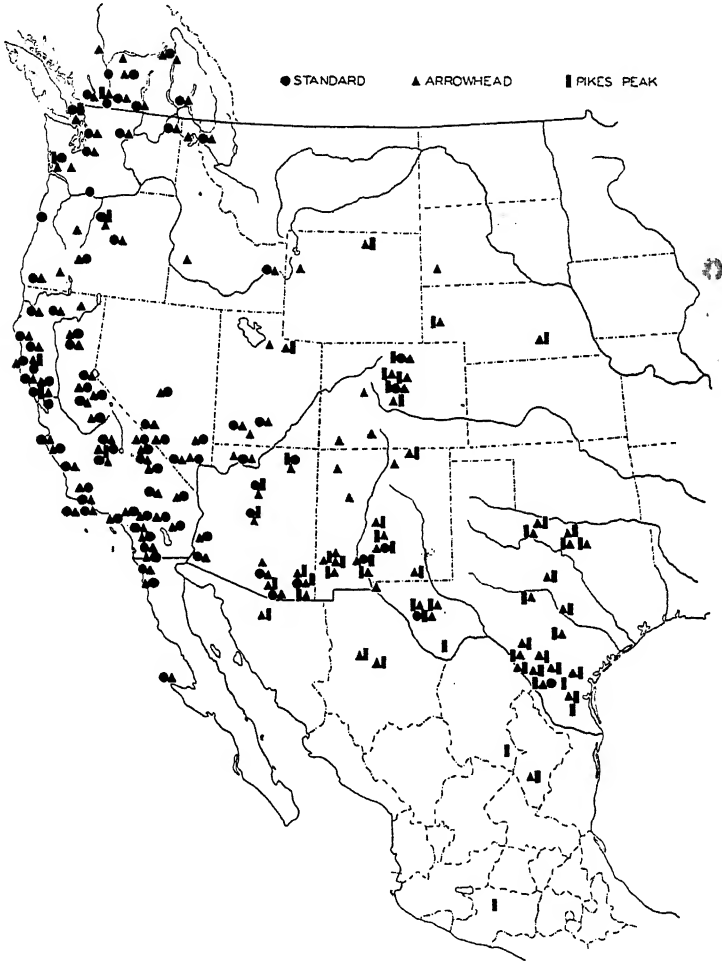

Fig. 7. Geographic distribution of the Santa Cruz phylad of gene arrangements in the third chromosome of *Drosophila pseudoobscura*.

arrangement in the populations inhabiting these countries. Its northern distribution limit is unknown, but its absence from the samples from Nuevo León and Chihuahua and from southern Arizona is probably significant, and indicates that Cuernavaca is found only or mainly below the Tropic of Cancer. Mammoth is a rare form, endemic to the eastern slopes of the Sierra Nevada and the adjacent ranges.

The distribution of the Tree Line phylad (fig. 8) taken as a whole resembles that of the whole Santa Cruz phylad (fig. 7), except that the former is widespread in the Rocky Mountains and Texas, whereas the latter is almost entirely absent in that area. The head of the phylad, Tree Line, has a wider distribution than any of its derivatives. Starting from Mexico and Guatemala, where it is
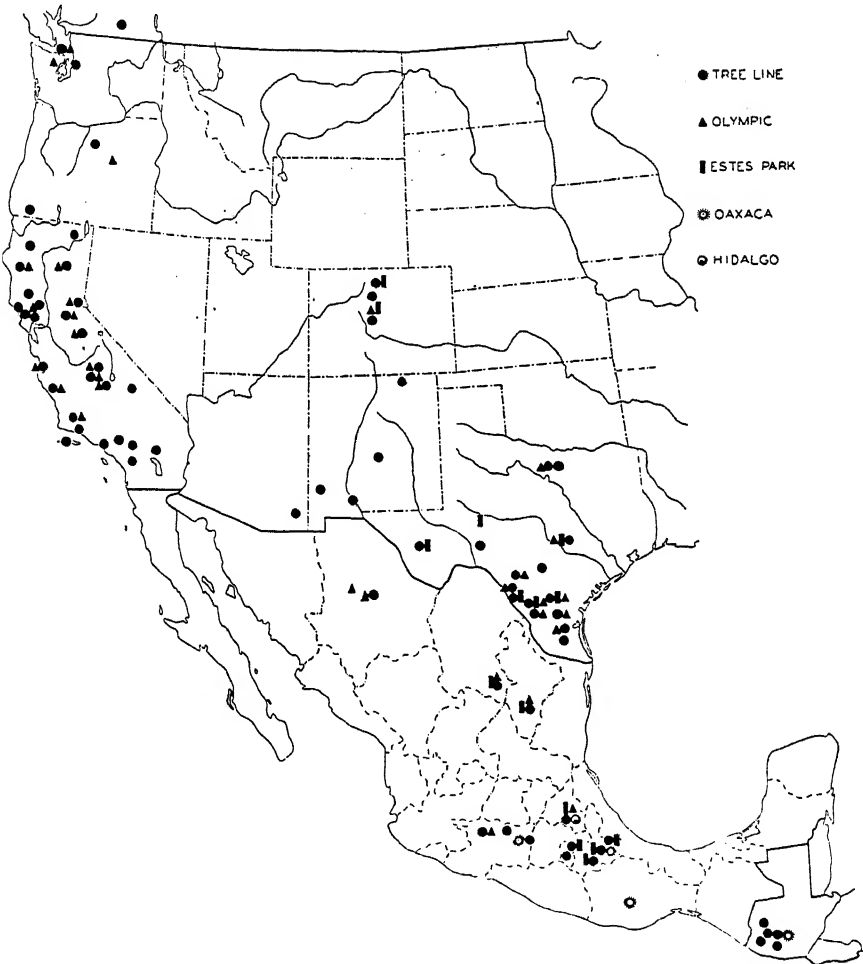
Fig. 8. Geographic distribution of the Tree Line phylad of gene arrangements in the third chromosome of *Drosophila pseudoobscura*.

one of the commonest gene arrangements, Tree Line extends northward in two enormous prongs, one along the Pacific coast and the other into the Rocky Mountains. Tree Line is, therefore, absent or rare only in the Colorado Plateau and the Basin and Range provinces. In California, western Mexico, and Guatemala, Tree Line coexists with its progenitor Santa Cruz. Olympic, derived from Tree Line, has approximately the same gross distribution as its parent.

Olympic is, however, much less frequent in most populations than Tree Line, and therefore is recorded less often. Only in the southern part of California does Olympic appear to be definitely absent, while Tree Line is present. No records of Olympic are known from Guatemala, but the population sample examined from that country is not large enough to make the absence of Olympic significant; it may be, of course, that Olympic has failed to cross the Isthmus of Tehuantepec, whereas Tree Line has accomplished this crossing. A most interesting, although unfortunately small, sample from Nuevo León shows Olympic and Tree Line to be the dominant arrangements in that locality; elsewhere, even in the rather near-by state of Chihuahua, they are not the main constituents of populations, although Tree Line is common in southern Mexico and Guatemala. Estes Park occurs in the Rocky Mountains, in Mexico, and, sporadically, in the north. The two other derivatives of Tree Line, Oaxaca and Hidalgo, are rare gene arrangements. Oaxaca has, however, been found in two places in southern Mexico as well as in Guatemala; Hidalgo is known from a single locality in Mexico.

The gene arrangements in *D. persimilis* belong to two closely related phylads centering on the Standard and Klamath arrangements respectively. The Standard itself is common in the southern part of the species area, that is in California, but rare or absent from Oregon to British Columbia (fig. 9). Mendocino is one of the derivatives of Standard, very common in the Coast Ranges of California and rarely found in the Sierra Nevada and in Oregon. The second derivative, Sequoia, is a rare arrangement recorded both in the Sierra Nevada and along the coast. The distribution of the third derivative, Klamath, is coextensive with that of *D. persimilis* itself, but whereas it is the dominant arrangement from British Columbia southward to Oregon, it becomes rare in California. Of the three derivatives of Klamath, Whitney is the most important. It is common, and in places dominant, in the Sierra Nevada, but it occurs sporadically on the coast of California and northward as far as British Columbia. The second derivative, Cowichan, occurs as an admixture in populations from British Columbia to the northern coastal part of California. Finally, the third derivative, Wawona, is an endemic in the part of the Sierra Nevada adjacent to the Yosemite National Park.

To summarize: none of the gene arrangements, and none of the phylads, of *D. pseudoobscura* is distributed throughout the species area. Nevertheless, some arrangements occur in populations that are geographically very remote and living in very dissimilar climatic and ecological regions. Thus, Arrowhead seems to be equally at home in the interior of British Columbia, along the humid Pacific coast, in the mountains of the Death Valley region, and on the plains of Texas. Tree Line manages to exist in the cool Pacific Northwest, in southern California, in Texas, and as far below the Tropic as Guatemala. In *D. persimilis,* which has a more restricted area, some gene arrangements are found throughout, but even here a considerable differentiation of the species population is apparent.
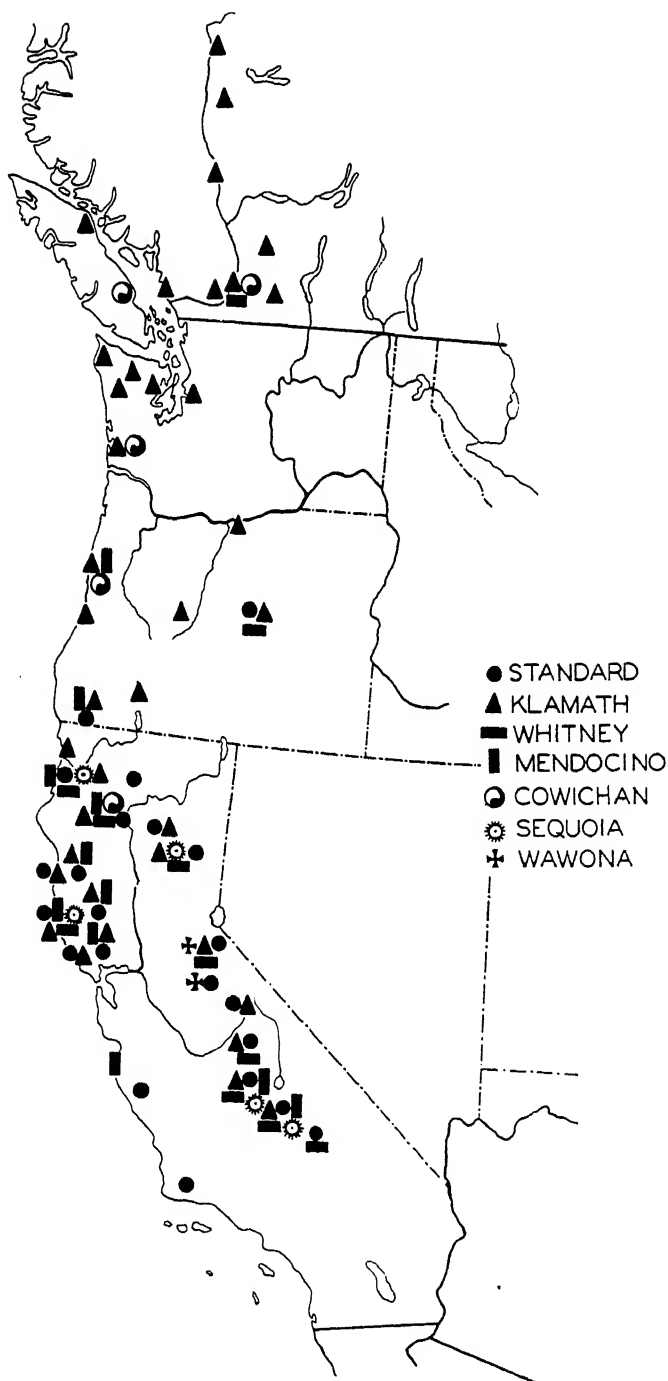
FIG. 9. Geographic distribution of the gene arrangements in the third chromosome of *Drosophila persimilis*.

GEOGRAPHIC DISTRIBUTION OF THE "SEX RATIO"

As stated above (p. 78), the "sex ratio" factors in *Drosophila pseudoobscura* or *D. persimilis* can be detected by either of two methods, based respectively on the following facts: first, males which carry the "sex ratio" produce offspring which consists of daughters and few or no sons, regardless of the genetic constitution of their mates; and, second, the "sex ratio" X chromosomes differ in gene arrangement from the normal X's. Both of these methods were used in analyzing the population samples from different geographical regions. The wild males were outcrossed to females from certain laboratory strains, and their offspring examined. If the offspring proved to be unisexual or nearly so, the male parent obviously carried a "sex ratio" X chromosome. The difference between normal and "sex ratio" cultures is great enough to make the classification reliable even without making complete counts of the flies (see Sturtevant and Dobzhansky, 1936a). Cytological examination of the offspring of wild females reveals the nature of the gene arrangement in their XR chromosomes. An observation on a single male larva permits the determination of the gene arrangement in one X chromosome present in the mother of that larva; an observation on a single female larva determines the nature of one maternal and one paternal X chromosome; examination of eight larvae in the offspring of a single wild female permits the gene arrangement in the two maternal and in one paternal X to be recorded. Since, however, the writer has only recently acquired a sufficient familiarity with the gene arrangement in the X chromosome to permit him easily to discriminate between "sex ratio" and normal X chromosomes in either species, the records of the frequencies of "sex ratio" made before 1939 were based entirely on genetic tests of wild males. In 1939 and thereafter the X chromosomes of wild males were examined genetically and those of wild females cytologically. Since no significant differences in the frequencies of "sex ratio" in females and males have been observed, the data obtained by both methods can be presented together.

A summary of the data for *D. pseudoobscura* is given in table 4, and of those for *D. persimilis* in table 5. The arrangement of localities in these tables follows the scheme of tables 1 to 3, dealing with the third chromosomes. Most of the old data on the frequencies of "sex ratio" published by Sturtevant and Dobzhansky (1936a) are included in tables 4 and 5, despite the fact that these older data are somewhat less exact than the newer ones, for the reason stated in the paper just referred to. The data of Dobzhansky (1939a) on Mexican and Guatemalan populations are not included. They can be summarized as follows: east-central Mexico, 126½ chromosomes tested, 19.4 per cent found to carry "sex ratio"; west-central Mexico, 32 chromosomes tested, 17.2 per cent "sex ratio"; Guatemala, 65½ chromosomes tested, 1.5 per cent "sex ratio." For an explanation of the fractions of chromosomes in these data see Dobzhansky (1939a).

Examination of table 4 shows that the frequency of the "sex ratio" in

D. pseudoobscura is unquestionably different in different regions. The average frequencies, and their standard errors, are as follows:

Region	Per cent	Region	Per cent
British Columbia	o	California and Nevada,	
Washington	o	Death Valley region....	10.1 ± 0.63
Oregon	o	Southern Utah	10.9 ± 3.10
Idaho, Montana, Wyoming,		Northern Arizona	16.2 ± 1.97
South Dakota, Nebraska,		Southern Arizona	18.6 ± 2.45
and northern Utah.....	o	Colorado	12.1 ± 2.60
California, northern Coast		New Mexico	14.4 ± 1.96
Ranges	9.05 ± 1.88	Texas	11.5 ± 0.95
Northeastern California and		Mexico, Nuevo León and	
Sierra Nevada	6.48 ± 1.26	Sonora	33.3 ± 12.2
California, southern Coast		Mexico, Chihuahua	6.8 ± 2.9
Ranges	7.00 ± 1.14	East-central Mexico	19.4 ± 3.52
California, southern section		West-central Mexico	17.2 ± 6.67
tion	14.7 ± 0.36	Guatemala	1.5 ± 1.5

"Sex ratio" is rare or absent in the northern part of the distribution area, and increases in frequency southward, dropping again to a low frequency in Guatemala. Its recorded frequency is highest in Mexico, Arizona, New Mexico, and southern California. The two samples from Chihuahua, Mexico, have, however, shown low frequencies of "sex ratio." The presence of this north-south gradient in the frequency of "sex ratio" has already been referred to by Sturtevant and Dobzhansky (1936a); the data recorded in table 4, which are more than fifty times as abundant as those available to Sturtevant and Dobzhansky, confirm the conclusion reached by these authors. The other inference of Sturtevant and Dobzhansky, that within a given area the frequency of "sex ratio" decreases with the altitude above sea level, is less certain. The most pertinent data in this case are those on the three localities on Mount San Jacinto, California, namely Keen Camp, Piñon Flat, and Andreas Canyon. The horizontal distances between these localities do not exceed 15 miles. Keen Camp lies at an elevation of 4300 feet in the yellow pine belt; Piñon Flat at 4000 in the piñon pine belt; and Andreas Canyon at 800 feet at the edge of the Colorado Desert. The frequencies of "sex ratio" are 16.3 ± 0.59, 12.3 ± 0.64, and 14.4 ± 0.63 per cent, respectively. The differences are significant (χ^2 is 17.82, which, for 2 degrees of freedom, may occur by chance less than once in 100 trials). The highest frequency of "sex ratio" is found in this case at the highest, and the lowest frequency at the intermediate elevation. The two samples from Mount Yollo Bolly (table 4) are not significantly different in the frequency of "sex ratio," but the apparent frequency is greater in the sample taken at the higher altitude. On the other hand, the samples taken at intermediate elevations in the Sierra Nevada (Lake Tahoe, Mariposa Grove, Atwell Mill, Mineral King, and Rattlesnake Meadow) seem to have fewer "sex ratio" chromosomes than samples taken at lower elevations (Deer Creek, Camino, Funston Meadow; table 4).

TABLE 4

"Sex ratio" in *Drosophila pseudoobscura*

SR, percentages of chromosomes which carry "sex ratio"; n, number of chromosomes examined

Locality	SR	n	Locality	SR	n
British Columbia			Funston Meadow	9.1	11
			Lone Pine Canyon, 1940....	7.1	28
Hope	0	9			
Princeton	0	12	*California, southern*		
Shuswap, Arrowhead, Nakusp, Kaslo *	0	14	*Coast Ranges*		
			Monterey	7.3	41
Washington			Santa Lucia Mts., 1935 *...	2.0	49
			Santa Lucia Mts., 1940	4.9	81
Friday Harbor	0	22	San Raphael Mts...........	7.4	54
Seattle	0	58	Santa Barbara and environs	8.0	275
Methow	0	69			
Willapa Bay	0	11	*California, Channel Islands*		
Metaline Falls *	0	7			
			Santa Cruz, 1940.........	20.8	72
Oregon			Santa Rosa, 1941.........	0	30
Cape Perpetua	0	2			
Selma	0	41	*California, southern section*		
Whitman Nat. Forest	0	13	Santa Monica	20.0	30
Spray	0	50	Pasadena *	22.2	27
			Keen Camp A	15.7	1125
California, northern			Keen Camp B	19.4	608
Coast Ranges			Keen Camp C	16.0	501
Coffee Creek	0	28	Keen Camp D	14.8	1024
Weott	20.0	10	Keen Camp E	17.0	711
Yollo Bolly, upper.........	16.7	12	Piñon Flat, A	12.0	1739
Yollo Bolly, lower.........	10.3	29	Piñon Flat, B	12.8	874
Mendocino	7.2	69	Andreas Canyon A ...	14.1	2115
Mt. St. Helena	10.7	84	Andreas Canyon B	15.0	957
			Borego	24.1	29
Northeastern California and			Joshua Tree Nat. Monument	15.8	19
Sierra Nevada			Chuckwalla	20.0	5
Alturas	0	8	Bagdad	20.0	5
Deer Creek	11.8	85			
Lake Tahoe	0	15	*Baja California*		
Camino	8.0	88	San Antonio Mesa	11.9	42
Mariposa Grove	2.8	36			
Stony Creek	14.3	14	*California and Nevada,*		
Atwell Mill	3.6	55	*Death Valley region*		
Mineral King	0	26	Panamint Mts. ‡	16.0	175
Rattlesnake Meadow	0	20	Wildrose A and B, 1937 †	8.1	136

* Data published in Sturtevant and Dobzhansky, 1936a.
† Data published in Dobzhansky and Queal, 1938.
‡ Data published in Koller, 1939.

TABLE 4—*Continued*

Locality	SR	n	Locality	SR	n
Wildrose A, May 1938 ‡....	22.7	44	*South Dakota*		
Wildrose A, October 1938...	14.3	28	Black Hills *	0	4
Wildrose A, 1939	12.1	280			
Wildrose A, 1940	18.3	82	*Nebraska*		
Wildrose B, 1939	7.3	177			
Wildrose B, 1940	2.8	71	Scottsbluff	0	4
Wildrose C, 1939	6.7	105	Gibbon	0	1
Wildrose C, 1940	13.9	36			
Wildrose D, 1939	14.5	69	*Colorado*		
Wildrose D, 1940	5.4	74	Estes Park	15.4	26
Magruder, Coso, Cottonwood,			Mt. Campbell	13.9	36
and Avawatz Mts.†	8.8	363	Pikes Peak	11.8	17
Grapevine, Kingston,			Mesa Verde	10.3	78
Charleston, and Sheep					
Mts.†	8.5	495	*New Mexico*		
Providence Mts. †	16.1	137	Raton Mesa	8.3	36
			Grant County	0	12
Idaho and Montana			Silver City	16.9	59
Coeur d'Alene *	0	11	Gila	5.9	17
Bitterroot Mts. *	0	3	Radium Springs	18.4	48
			Las Cruces	17.9	39
Utah			Capitan	13.3	30
Salt Lake City, 1941........	0	4	Hondo	15.2	79
Uinta Mts.	0	6			
Cedar City *	0	6	*Texas*		
Zion Nat. Park *	50.0	8	Marfa	7.4	27
Bryce Nat. Park..........	8.0	87	Limpia Canyon and Davis		
			Mts.	23.3	30
Arizona			Chisos Mts.	10.7	28
Kaibab Nat. Forest........	10.5	86	Fort Worth	25.0	4
Cape Royal	10.7	84	Arlington	25.0	4
Flagstaff	23.2	82	Aldrich, March 1939	14.0	57
Black Mesa	17.9	28	Aldrich, April 1939........	12.5	425
Prescott	21.1	71	Aldrich, May 1939	10.7	121
Chiricahua Mts.	19.8	96	Aldrich, Autumn 1939	11.5	26
Williams Ranch and Ashton			Aldrich, March 1940	7.5	305
Draw	15.4	39	Aldrich, April 1940	14.8	169
Huachuca Mts.	8.0	50	Aldrich, May 1940	9.1	22
Tucson	25.0	8	Aldrich, April 1941........	5.6	18
Sonoita	33.3	30			
Castle Dome	0	6	*Mexico*		
Yuma	25.0	24	San Josecito, Nuevo León ..	33.3	12
			Chihuahua City, Chihuahua	6.2	192
Wyoming			Santa Clara Mts., Chihuahua	10.0	30
Big Horn Mts. *......... ..	0	3	Magdalena, Sonora	33.3	3

* Data published in Sturtevant and Dobzhansky, 1936*a*.
† Data published in Dobzhansky and Queal, 1938.
‡ Data published in Koller, 1939.

The north-south gradient in the frequency of "sex ratio" makes it tempting to suppose that this frequency is determined by climatic conditions, and by differences of temperature. But the rarity of the "sex ratio" in Guatemala and the lack of a definite correlation between the frequency of "sex ratio" and the altitude of the locality seem to contradict this hypothesis, although there may exist other climatic factors with which the frequency of "sex ratio" might show a more definite correlation. An alternative possibility is that the high frequency of "sex ratio" in Mexico and the adjacent part of the United States

TABLE 5

"Sex ratio" in *Drosophila persimilis*

SR, percentage of chromosomes which carry "sex ratio"; n, number of chromosomes examined

Locality	SR	n	Locality	SR	n
British Columbia			Eureka *	20.0	15
			Coffee Creek	23.1	13
Hope	0	9	Weott	25.0	12
Princeton	0	12	Shelter Cove *	16.7	12
			Yollo Bolly, upper........	33.3	6
Washington			Yollo Bolly, lower........	50.0	4
Seattle	0	26	Mendocino	7.0	71
Willapa Bay	0	19	Monterey	0	4
			Santa Lucia Mts.*.........	0	8
Oregon					
Cape Perpetua	13.3	30	*Northeastern California and*		
Newport *	0	8	*Sierra Nevada*		
Reedsport *	7.1	13	Mt. Lassen *	28.6	7
Gold Beach *	21.4	14	Deer Creek	26.7	15
Selma	25.0	24	Stony Creek	14.3	14
Oregon Caves *	33.3	6	Atwell Mill	7.7	26
			Mineral King	16.0	25
California, Coast Ranges			Rattlesnake Meadow	14.6	48
Klamath *	30.0	20	Funston Meadow	21.1	38
Orick	9.5	42	Lone Pine Canyon	4.8	42

* Data published in Sturtevant and Dobzhansky, 1936a.

results from historical causes, and that the gradient referred to is in some way correlated with the geographic distribution of the various gene arrangements in the third chromosome, which likewise show no clear environmental correlations.

"Sex ratio" in *D. persimilis* (table 5) is rare or absent in British Columbia and in Washington. In Oregon, in the northern Coast Ranges of California, and in the Sierra Nevada, the "sex ratio" is rather common, but our material from the southern Coast Ranges of California (Monterey, Santa Lucia; table 5) is far too limited to determine the frequency of the "sex ratio" in that region. The data, therefore, may or may not be consistent with the assumption that in

D. persimilis, as in *D. pseudoobscura,* there is a north-south gradient in the frequency of the "sex ratio." The available information is likewise insufficient to demonstrate any possible connection between this gradient and climatic or other factors.

The Intra-populational Equilibrium

A normal diploid individual of *Drosophila* carries every chromosome in duplicate, except that each male has a single X and a single Y chromosome. Within a given population, two, or as many as seven, types of chromosomes may occur which differ in their gene arrangement. Provided that females and males which carry chromosomes with different arrangements can mate and produce offspring, the two chromosomes of a pair present in an individual may have either the same or different arrangements. That is, a given individual may be either a structural homozygote or a structural heterozygote. The frequency of these structural homozygotes and heterozygotes within a given population depends on two main factors. First, the mating of flies of different chromosome constitution may be selective or it may be at random; second, the viability of some or of all homozygotes may be similar to or different from that of the heterozygotes. Let it be assumed that the gene arrangements A, B, and C occur in the third chromosomes of a certain population. The frequencies of gametes which carry these arrangements are p, q, and r respectively $(p+q+r=1)$. Provided (1) that the matings are at random with respect to the gene arrangement, (2) that the survival rates of all types of zygotes are alike, and (3) that the origin of a given gene arrangement is seldom, if ever, repeated, the relative frequencies of different types of zygotes will, according to Hardy's law, follow the expansion $(p+q+r+ \ldots)^2$. For three gene arrangements A, B, and C, the expected frequencies of homo- and heterozygotes would be as follows:

Homozygotes		Heterozygotes	
AA	p^2	AB	$2pq$
BB	q^2	AC	$2pr$
CC	r^2	BC	$2qr$

Any deviation from the above frequencies would indicate that the conditions of genetic equilibrium are lacking in the population in which this deviation is observed.

The numbers of third chromosomes with various gene arrangements found in the population samples examined are shown in tables 1 to 3. Knowing the total number of chromosomes in each sample, it is easy to calculate the gametic frequencies p, q, r . . . of each gene arrangement in the sample. The expected zygotic frequencies can then be compared with the observed ones, which are recorded in the raw data on the basis of which tables 1 to 3 were constructed (cf. p. 79). On account of the labor involved, it has not seemed advisable to calculate the expected zygotic frequencies for all the samples,

regardless of size. Only those of samples in which more than 50 zygotes (100 gametes) were recorded have been computed. Fortunately, samples of this size are available from many parts of the distribution area of the species, and contain a variety of gene arrangements. The observed and the expected zygotic frequencies in these samples are presented in tables 6 to 9. Four separate tables are needed because different sets of gene arrangements are found in different samples. In order not to make the tables unwieldy in size, the rare arrangements have not been included in them; this accounts for the failure of the expected numbers of homo- and heterozygotes to add up to the totals of the observed numbers in some of the samples. So far as possible, only samples collected in a single day or within a short time period in an area not exceeding ¼ mile in diameter are included in the tables. This is important because of the necessity of avoiding samples which might be composites of several breeding units with different gametic frequencies of gene arrangements. In such samples an excess of homozygotes might be observed. Additional data on the observed and expected frequencies of homozygotes and heterozygotes for gene arrangements in the third chromosome have been published by Dobzhansky and Queal (1938) and by Koller (1939).

A glance at the data in tables 6 to 9 suffices to show that structural heterozygotes are not only present but very common in natural populations. As a matter of fact, in many samples considerably more than half of the individuals are heterozygotes. In general, the agreement of the observed and the expected frequencies is close. We are justified in concluding, therefore, at least as a first approximation, that natural populations of *Drosophila pseudoobscura* are panmictic, and that all homo- and heterozygous combinations of the third-chromosome gene arrangements are equal in viability. Deviations from these conditions would be too small to be detected within individual samples of the size we have in our material, but the material taken as a whole offers an opportunity for their detection, if they are in fact present.

The χ^2 values have been computed for each pair of observed and expected figures of total frequencies of homozygotes in tables 6 to 9. Sixty-five such comparisons are possible. The highest χ^2 value turned out to be 3.343 (Moore's Ranch, table 6). For 1 degree of freedom, such or a greater value should occur by chance in between 5 and 10 out of 100 trials. Since it was actually observed only once in 65 trials, the difference between the observed and the expected numbers of homozygotes at Moore's Ranch certainly cannot be considered significant. Values of χ^2 exceeding unity are expected to occur by chance in about 30 out of 100 trials; in our material they occurred in 10 out of 65 trials, that is, even less frequently than expected. In all the samples reported in tables 6 to 9 a total of 1614 homozygotes and 2390 heterozygotes was observed. Adding up the expected numbers of homozygotes in all the samples, we obtain the figure 1659.0. The χ^2 equals 1.221, and is not significant. Adding also the materials published by Dobzhansky and Queal (1938) and by Koller (1939), the observed total rises to 2401 and the expected to 2446.8.

TABLE 6

OBSERVED AND EXPECTED NUMBERS OF HOMO- AND HETEROZYGOTES FOR GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura*

ST, Standard; AR, Arrowhead; CH, Chiricahua; TL, Tree Line; SC, Santa Cruz; OL, Olympic; HOM, total homozygotes; HET, total heterozygotes.

Locality		ST/ST	AR/AR	CH/CH	TL/TL	SC/SC	OL/OL	ST/AR	ST/CH	ST/TL	ST/SC	ST/OL	AR/CH	AR/TL	AR/SC	AR/OL	CH/TL	CH/OL	CH/SC	TL/SC	TL/OL	SC/OL	HOM	HET
Mt. St. Helena	Obs.	7	2	0	2	2	0	8	5	6	4	1	4	2	3	1	3	0	0	2	2	0	13	41
	Exp.	6.6	2.2	0.7	1.7	1.3	0.1	7.6	4.2	6.8	4.5	1.5	2.4	3.9	2.6	0.9	2.2	0.5	1.4	2.3	0.8	0.5	12.6	42.0
Santa Lucia Mts.	Obs.	12	2	0	0	1	0	11	8	1	9	0	3	0	3	0	1	1	0	0	0	0	15	37
	Exp.	13.5	2.1	0.8	0.02	1.0	0.01	10.5	6.6	1.0	7.2	0.5	2.6	0.4	2.8	0.2	0.3	0.1	1.8	0.3	0.02	0.1	17.4	34.5
Moore's Ranch	Obs.	20	4	1	0	1	0	3	8	0	4	0	3	1	2	0	2	0	2	0	0	0	26	25
	Exp.	14.8	1.4	1.4	0.04	0.5	0	9.2	9.2	1.6	5.4	0	2.8	0.5	1.7	0	0.5	0	1.7	0.3	0	0	18.2	32.8
Mission Canyon	Obs.	10	3	5	0	0	0	12	6	4	4	0	3	5	2	0	3	0	0	0	0	0	18	39
	Exp.	9.3	3.5	2.1	0.6	0.1	0	11.3	8.9	4.8	2.3	0	5.4	2.9	1.4	0	2.3	0	1.1	0.6	0	0	15.7	41.2
Deer Creek	Obs.	5	19	0	0	0	0	21	1	0	0	0	3	3	1	2	0	0	0	0	1	0	24	32
	Exp.	5.0	22.0	0.1	0.1	0.00	0.04	18.1	1.2	1.2	0.3	0.9	2.6	2.6	0.6	1.9	0.1	0.01	0.04	0.04	0.01	0.03	27.1	29.3
Camino	Obs.	4	4	0	0	3	0	10	2	6	2	1	1	2	5	3	2	0	2	3	2	2	11	43
	Exp.	3.9	3.9	0.2	1.0	1.9	0.3	7.8	1.9	4.0	5.4	2.1	1.9	4.0	5.4	2.2	1.0	0.5	1.3	2.8	1.1	1.5	11.2	42.8

TABLE 7

OBSERVED AND EXPECTED NUMBERS OF HOMO- AND HETEROZYGOTES FOR GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura*

ST, Standard; AR, Arrowhead; PP, Pikes Peak; CH, Chiricahua; TL, Tree Line; HOM, total homozygotes; HET, total heterozygotes. One zygote with the Estes Park arrangement (Marfa sample) is disregarded

Locality		ST/ST	AR/AR	PP/PP	CH/CH	TL/TL	ST/AR	ST/PP	ST/CH	ST/TL	AR/PP	AR/CH	AR/TL	PP/CH	PP/TL	CH/TL	HOM	HET
Methow	Obs.	12	10	0	0	0	27	0	1	0	0	0	0	0	0	0	22	28
	Exp.	13.5	11.0	0	0.01	0	24.4	0	0.5	0	0	0.5	0	0	0	0	24.6	25.4
Prescott	Obs.	2	33	0	0	0	6	0	1	0	0	7	0	1	0	0	35	15
	Exp.	0.6	31.2	0.01	0.4	0	8.7	0.1	1.0	0	0.8	7.1	0	0.1	0	0	32.2	17.8
Raton	Obs.	0	30	2	0	0	0	0	0	0	16	1	1	0	0	0	32	18
	Exp.	0	30.4	2.0	0.005	0.005	0	0	0	0	15.6	0.8	0.8	0.2	0.2	0.01	32.4	17.6
Hondo	Obs.	0	13	2	1	0	0	0	0	0	27	4	1	2	1	0	16	35
	Exp.	0	16.6	5.6	0.3	0.02	0	0	0	0	19.2	4.7	1.2	2.7	0.7	0.2	22.5	28.5
Marfa	Obs.	0	7	17	0	1	0	2	0	0	30	2	1	2	5	0	25	42
	Exp.	0.01	8.2	19.9	0.1	0.2	0.7	1.1	0.1	0.1	25.9	1.4	2.8	2.2	4.4	0.2	28.4	38.9

TABLE 8

OBSERVED AND EXPECTED NUMBERS OF HOMO- AND HETEROZYGOTES FOR GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura* (ALDRICH) AND OF *Drosophila persimilis* (ORICK, MENDOCINO)

PP, Pikes Peak; AR, Arrowhead; TL, Tree Line; OL, Olympic; EP, Estes Park; ST, Standard; K, Klamath; M, Mendocino; SE, Sequoia; W, Whitney; HOM, total homozygotes; HET, total heterozygotes

Aldrich:

Locality		PP/PP	AR/AR	TL/TL	OL/OL	EP/EP	PP/AR	PP/TL	PP/EP	PP/OL	AR/TL	AR/OL	AR/EP	TL/OL	TL/EP	OL/EP	HOM	HET
March 1939	Obs.	43	2	0	0	0	27	8	1	0	1	0	0	0	0	0	45	37
	Exp.	45.5	3.1	0.3	0	0.00	23.8	6.7	0.7	0	1.8	0	0.2	0	0.05	0	48.9	33.3
April 1939	Obs.	79	3	0	0	0	53	14	5	1	2	0	1	0	0	0	82	75
	Exp.	84.8	5.9	0.4	0.00	0.04	44.8	11.8	3.7	0.7	3.1	0.2	1.0	0.05	0.3	0.02	91.2	65.5
March 1940	Obs.	70	8	2	0	0	73	15	0	7	5	3	0	0	0	0	80	103
	Exp.	75.4	12.8	0.8	0	0	62.3	15.5	0	6.3	6.4	2.6	0	0.6	0	0	89.2	93.8
April 1940	Obs.	47	7	0	0	0	38	15	1	3	2	0	0	1	0	0	54	60
	Exp.	50.0	6.4	0.7	0.03	0.00	35.6	12.1	0.6	2.7	4.2	1.0	0.2	0.3	0.1	0.02	57.1	56.9

Locality		K/K	M/M	ST/ST	SE/SE	W/W	K/M	K/ST	K/SE	K/W	ST/M	M/SE	M/W	ST/SE	ST/W	SE/W	HOM	HET
Orick	Obs.	11	17	0	0	0	22	0	1	1	1	0	0	0	0	0	28	25
	Exp.	9.9	15.3	0.01	0.01	0.01	24.7	0.46	0.5	0.5	0.6	0.6	0.6	0.01	0.01	0.01	25.3	27.8
Mendocino	Obs.	4	30	0	0	0	13	3	0	0	4	1	0	0	1	0	34	22
	Exp.	2.6	27.9	0.3	0.00	0.00	16.7	1.71	0.2	0.2	5.6	0.7	0.7	0.7	0.7	0.01	30.0	26.0

TABLE 9

OBSERVED AND EXPECTED NUMBERS OF HOMO- AND HETEROZYGOTES FOR GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura*

ST, Standard; AR, Arrowhead; CH, Chiricahua; TL, Tree Line; HOM, total homozygotes; HET, total heterozygotes. Zygotes with very rare gene arrangements (Santa Cruz, Mammoth) disregarded

Station		ST/ST	AR/AR	CH/CH	TL/TL	ST/AR	ST/CH	ST/TL	AR/CH	AR/TL	CH/TL	HOM	HET
Wildrose A:													
1939	Obs.	15	24	4	0	24	7	5	14	1	0	43	51
	Exp.	11.8	19.9	2.2	0.1	30.6	10.2	2.1	13.3	2.8	0.9	34.0	60.0
1940	Obs.	4	10	2	0	8	10	0	13	5	1	16	37
	Exp.	3.2	9.9	3.7	0.2	11.2	6.9	1.5	12.1	2.6	0.6	17.0	35.9
Wildrose B:													
1939	Obs.	9	22	1	0	32	6	2	16	5	2	32	63
	Exp.	8.8	24.8	1.8	0.2	29.6	7.9	2.7	13.3	4.6	1.2	35.6	59.3
1940	Obs.	4	16	1	0	14	5	0	9	0	0	21	28
	Exp.	3.7	15.7	1.3	0	15.1	4.3	0	9.0	0	0	20.5	28.4
Wildrose C, 1939	Obs.	5	10	1	0	22	5	0	6	1	0	16	34
	Exp.	6.9	12.0	0.9	0.01	18.1	4.8	0.4	6.4	0.5	0.1	19.7	30.3
Wildrose D:													
1939	Obs.	11	6	1	0	21	8	1	1	0	1	18	32
	Exp.	13.5	5.8	0.7	0.02	17.7	6.2	1.0	4.1	0.7	0.2	20.0	30.0
1940	Obs.	7	4	3	0	18	6	1	8	3	0	14	36
	Exp.	7.6	6.8	2.0	0.1	14.4	7.8	1.6	7.4	1.5	0.8	16.5	33.5
Keen Camp A:													
June 1939	Obs.	7	4	8	0	8	16	4	17	1	1	19	47
	Exp.	6.7	4.4	9.5	0.1	10.8	15.9	1.9	12.9	1.5	2.2	20.7	45.3
July 1939	Obs.	7	7	9	1	16	11	1	8	1	3	24	40
	Exp.	6.9	6.0	6.2	0.2	12.8	13.1	2.3	12.2	2.1	2.2	19.3	44.7

(*Continued on following page*)

TABLE 9—Continued

Station	ST/ST	AR/AR	CH/CH	TL/TL	ST/AR	ST/CH	ST/TL	AR/CH	AR/TL	CH/TL	HOM	HET
Keen Camp A—continued:												
April 1940 Obs.	10	1	7	0	8	17	0	13	2	0	18	40
April 1940 Exp.	8.8	2.6	8.4	0.02	9.6	17.2	0.8	9.4	0.4	0.8	19.9	38.1
May 1940 Obs.	6	-1	14	0	8	11	0	7	0	2	21	28
May 1940 Exp.	5.1	1.5	11.5	0.02	5.4	15.4	0.6	8.2	0.3	1.0	18.1	30.9
June 1940 Obs.	4	1	6	0	13	11	1	15	0	2	11	42
June 1940 Exp.	5.2	4.2	7.5	0.04	9.4	12.5	0.9	11.3	0.8	1.1	17.0	36.0
July 1940 Obs.	5	4	9	0	9	16	1	6	0	0	18	32
July 1940 Exp.	6.5	2.6	8.0	0.01	8.3	14.4	0.4	9.2	0.2	0.4	17.1	32.9
August 1940 Obs.	5	4	8	0	15	11	1	7	1	2	17	37
August 1940 Exp.	6.4	4.4	6.00	0.1	10.6	12.3	1.4	10.3	1.2	1.3	16.9	37.1
May 1941 Obs.	6	5	9	0	6	12	2	20	0	2	20	42
May 1941 Exp.	4.1	5.2	10.9	0.1	9.3	13.4	1.0	15.1	1.2	1.7	20.3	41.7
June 1941 Obs.	6	2	6	0	9	16	0	8	1	2	14	36
June 1941 Exp.	6.8	2.4	7.2	0.1	8.1	14.0	1.1	8.4	0.7	1.1	16.5	33.4
April 1942 Obs.	8	0	4	0	10	15	5	6	2	1	12	39
April 1942 Exp.	10.4	1.6	4.4	0.3	8.1	13.5	3.6	5.3	1.4	2.3	16.7	34.3
Piñon Flat A:												
May 1939 Obs.	7	7	5	0	14	7	2	13	0	2	19	38
May 1939 Exp.	5.7	7.7	4.5	0.1	13.2	10.2	1.2	11.8	1.4	1.1	18.0	38.9
June 1939 Obs.	7	8	3	0	12	11	0	13	2	1	18	39
June 1939 Exp.	6.2	8.0	4.1	0.04	14.1	10.1	1.0	11.5	1.1	0.81	18.4	38.6
September 1939 Obs.	12	3	5	0	10	10	3	4	1	0	20	28
September 1939 Exp.	12.0	2.2	2.9	0.1	10.3	11.8	2.0	5.0	0.8	1.0	17.2	30.8
October 1939 Obs.	24	5	2	0	15	8	3	7	1	1	31	35
October 1939 Exp.	21.0	4.1	1.5	0.1	18.5	11.3	2.8	4.9	1.2	0.7	26.7	39.4
March 3, 1940 Obs.	14	1	6	0	8	10	3	5	1	2	21	29
March 3, 1940 Exp.	12.1	1.3	4.2	0.2	7.8	14.2	2.9	4.6	1.0	1.7	17.7	32.3

TABLE 9—Continued

Station		ST/ST	AR/AR	CH/CH	TL/TL	ST/AR	ST/CH	ST/TL	AR/CH	AR/TL	CH/TL	HOM	HET
Piñon Flat A—continued:													
March 29, 1940	Obs	6	2	4	0	15	15	1	9	0	3	12	43
	Exp	8.9	3.4	5.4	0.1	11.1	13.8	1.6	8.6	1.0	1.2	17.8	37.3
May 1940	Obs	5	5	4	0	7	15	0	13	2	0	14	37
	Exp	5.0	5.0	6.4	0.02	10.1	11.3	0.6	11.3	0.6	0.7	16.4	34.7
September 1940	Obs	6	3	7	0	10	13	1	10	0	2	16	36
	Exp	6.2	3.3	7.3	0.04	9.0	13.5	1.0	9.8	0.8	1.1	16.8	35.2
March 1941	Obs	19	0	4	0	8	12	4	2	2	3	23	31
	Exp	17.5	0.7	3.1	0.4	6.8	14.6	5.1	2.8	2	2.1	21.6	32.4
April 1941	Obs	18	0	2	0	16	9	3	5	1	1	20	35
	Exp	18.5	2.2	1.6	0.1	12.8	10.9	3.2	3.7	1.1	0.9	22.4	32.6
May 1941	Obs	12	3	3	0	11	8	1	9	2	1	18	32
	Exp	9.7	3.9	2.9	0.1	12.3	10.6	1.8	6.7	1.1	1.0	16.6	33.4
June 1941	Obs	6	7	5	0	9	7	1	13	2	0	18	32
	Exp	4.2	7.2	4.5	0.1	11.0	8.7	0.9	11.4	1.1	0.90	16.0	34.0
August 1941	Obs	13	2	2	0	12	17	1	7	0	0	17	37
	Exp	14.6	2.4	3.7	0.00	11.8	14.6	0.5	5.9	0.2	0.3	20.6	33.3
April 1942	Obs	14	2	0	0	11	13	2	5	2	2	16	35
	Exp	14.3	2.4	2.0	0.2	11.7	10.6	3.2	4.3	1.3	1.2	18.8	32.3
Andreas Canyon A:													
April 1939	Obs	30	2	1	0	10	5	2	0	0	0	33	18
	Exp	28.7	0.9	0.2	0.02	10.3	5.1	1.5	0.9	0.3	0.1	29.9	18.3
September 1939	Obs	17	1	4	0	12	6	0	6	2	1	22	27
	Exp	14.3	2.4	2.2	0.04	11.6	11.1	1.6	4.5	0.6	0.6	18.9	30.1
October 1939	Obs	15	5	1	0	18	4	2	5	1	0	21	30
	Exp	14.3	5.6	0.6	0.04	17.8	6.0	1.6	3.7	1.0	0.3	20.5	30.5
December 1939	Obs	11	6	1	0	14	10	2	7	0	1	18	34
	Exp	11.1	5.2	1.9	0.04	15.2	9.2	1.4	6.3	1.0	0.6	18.3	33.7

TABLE 9—*Continued*

Station		ST/ST	AR/AR	CH/CH	TL/TL	ST/AR	ST/CH	ST/TL	AR/CH	AR/TL	CH/TL	HOM	HET
Andreas Canyon A—*continued*:													
January 1940	Obs.	13	5	0	0	18	9	1	5	0	1	18	34
	Exp.	14.1	5.3	1.0	0.02	17.3	7.6	1.1	4.7	0.7	0.3	20.4	31.6
February 1940	Obs.	18	6	0	0	22	6	3	1	1	0	24	33
	Exp.	19.7	5.7	0.2	0.1	21.2	4.1	2.4	2.2	1.3	0.2	25.7	31.3
March 2, 1940	Obs.	27	3	0	0	23	7	5	5	1	0	30	41
	Exp.	27.9	4.3	0.5	0.1	21.9	7.6	3.7	3.0	1.5	0.5	32.8	38.2
March 28, 1940	Obs.	23	3	1	1	11	12	1	2	0	1	28	27
	Exp.	22.3	1.7	1.3	0.1	12.1	10.8	2.5	3.0	0.7	0.6	25.3	29.7
April 1940	Obs.	8	1	3	0	13	13	2	7	2	0	12	37
	Exp.	10.1	2.9	3.4	0.1	10.8	11.7	1.8	6.2	1.0	0.6	16.5	32.2
October 1940	Obs.	26	3	0	1	11	3	3	3	0	1	30	21
	Exp.	23.0	2.0	0.3	0.2	13.7	4.8	4.1	1.4	1.2	0.4	25.4	25.6
February 1941	Obs.	11	3	2	0	20	6	1	6	1	0	16	34
	Exp.	12.0	5.5	1.3	0.02	16.2	7.8	1.0	5.3	0.7	0.32	18.7	31.3
March 1941	Obs.	26	1	0	0	14	15	0	1	0	0	27	30
	Exp.	28.7	1.3	1.1	0	12.1	11.3	0	2.4	0	0	31.1	25.9
April 1941	Obs.	24	1	2	0	14	7	1	1	0	0	27	23
	Exp.	24.5	1.5	0.7	0.01	11.9	8.4	0.7	2.0	0.2	0.1	26.7	23.3
September 1941	Obs.	17	2	1	0	23	15	1	1	1	0	20	31
	Exp.	21.8	3.5	1.3	0.01	17.4	10.8	1.2	4.3	0.5	0.3	26.6	34.4
November 1941	Obs.	21	2	0	0	12	8	3	2	0	1	23	26
	Exp.	21.8	1.6	0.6	0.1	11.9	7.3	2.6	2.0	0.7	0.4	24.1	24.9
December 1941	Obs.	12	6	2	0	16	7	1	4	2	0	20	30
	Exp.	11.5	5.8	1.1	0.04	16.3	7.2	1.4	5.1	1.0	0.5	18.5	31.5
January 1942	Obs.	24	7	1	0	24	12	3	0	2	0	32	41
	Exp.	25.9	5.5	0.7	0.1	23.8	8.4	3.0	3.8	1.4	0.5	32.2	40.8
February 1942	Obs.	20	1	3	0	14	7	3	2	0	0	24	26
	Exp.	20.5	1.6	1.1	0.04	11.5	9.6	1.9	2.7	0.5	0.5	23.3	26.7
April 1942	Obs.	29	2	1	0	9	7	1	0	1	1	32	19
	Exp.	27.8	1.0	0.5	0.04	10.3	7.3	2.2	1.4	0.4	0.3	29.3	21.8

The difference is again not significant. The observed values fit the expectation very well indeed.

So perfect a fit is, in a way, astonishing. Although there are no theoretical reasons to expect great deviations from panmixia and from uniform viability in our material, there are several causes which might produce perceptible deviations. First, there is the possibility of very local inbreeding, such as brother-sister mating, in the places where the flies hatch from the pupae (cf. Dobzhansky and Wright, 1941; Wright, Dobzhansky, and Hovanitz, 1942). Local inbreeding would cause an excess of homozygotes. Second, structural homozygotes may, in some populations, be less viable than the heterozygotes, on account of recessive mutants with deleterious effects carried in the chromosomes. Such mutants are known to be very common in natural populations. Lastly, the seasonal alterations in the frequencies of some gene arrangements (see below) indicate that certain types of zygote have, at least at times, a viability inferior to others. If the three types of zygote, AA, AB, and BB, survive in a ratio of $1:(1-hs):(1-s)$, the distribution demanded by Hardy's formula:

$$q^2 AA, \; 2q \, (1-q) \; AB, \; (1-q)^2 \; BB$$

is transformed into:

$$q^2 AA, \; 2q \, (1-q) \, (1-hs) \; AB, \; (1-q)^2(1-s) \; BB$$

If s is positive and $h=0$ (i.e., the structural homozygote BB is discriminated against), the heterozygotes must be more frequent than they should be according to Hardy's formula. If s is negative (i.e., the homozygote BB is favored), there should be an excess of homozygotes. If h lies between 0 and 1 (incomplete dominance), excesses of one or the other class might be observed. Since the changes with time in certain populations are very appreciable (see below), the s values would be large enough to produce deviations detectable in material even as extensive as ours.[1] The lack of any evidence of disturbances of Hardy's ratios may be caused, in part, by the considerable variety of gene arrangements present in most populations: the deficiency of certain homo- or heterozygotes may be counterbalanced by a simultaneous excess of others. Furthermore, a part of the zygotes recorded were larvae from the offspring of wild females fertilized in nature by wild males (see the chapter on methods). Since these larvae developed in the laboratory, their survival ratios may have been equalized. This consideration is not applicable to that part of the material which deals with the determination of the zygotic constitution of wild males, but in the combined samples the deviations are no longer perceptible. The problem deserves further study in material collected especially for that purpose. But the evidence at hand suggests that the natural populations of *Drosophila pseudoobscura* are panmictic and that the various gene arrangements in the third chromosome are of equal viability.

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[1] The writer is under obligation to Mr. H. Levene for discussions regarding this analysis.

TEMPORAL CHANGES IN THE COMPOSITION OF POPULATIONS

The degree to which the relative frequencies of the gene arrangements of a given population are constant can be studied by comparing samples taken at the same collecting station at different times. Dobzhansky and Sturtevant (1938) examined the third chromosomes in two samples of the population then inhabiting a certain part of San Gabriel Canyon, California, taken five months apart, in November 1936 and in April 1937 respectively. Despite the smallness of these samples, the data for which are reproduced in table 1, the frequency of the Standard arrangement was significantly greater in April, and the frequencies of the Chiricahua and Tree Line arrangements were greater in November. The frequency of Arrowhead underwent no significant change. This collecting station was located in a territory much disturbed by man, and the unintentional introduction of flies from other localities did not seem to be excluded. Hence, the results were uncertain. However, other indications of fluctuations in the relative frequencies of the gene arrangements of natural populations soon appeared.

Koller (1939) examined a population sample taken on May 26, 1938 in Wildrose Canyon, Panamint Mountains, California, in a territory which constitutes a part of the somewhat larger area sampled on May 20, 1937 by Dobzhansky. The two samples were significantly different (cf. tables 1 and 10). On the other hand, the population of Lone Pine Canyon (Mount Whitney) showed no appreciable change between 1937 and 1938. Wildrose Canyon was accordingly revisited on October 2, 1938, June 9 and 10, 1939, and May 30 and 31, 1940. In 1939 and 1940 samples were taken at four collecting stations designated as Wildrose A, B, C, and D. Each station comprised a territory about 100 meters in diameter. Wildrose A corresponds to the territory in which Koller's 1938 sample was taken. Wildrose B was approximately ⅓ mile up the canyon from A; the 1937 sample came from an area including A and B, as well as the intervening territory. Wildrose C and D were about ¼ mile from each other, and approximately 3 miles distant from A and B. A sample was taken also in Lone Pine Canyon in July 1940, the same month in which this station was sampled in 1937 and 1938. The primary data are presented in table 1, and the percentage frequencies of the gene arrangements are given in table 10.

Examination of table 10 suggests that between 1938 and 1940 no change comparable in extent with that which took place between 1937 and 1938 occurred. It is true that some gene arrangements found in one year were not recovered in the next, but these arrangements are rare in that region, and their failure to appear throughout may well have been due to sampling errors. A more rigorous test of the uniformity of the samples taken in different years at the same station is furnished by a statistical analysis of the data. If we assume that the apparent changes were caused by sampling errors, the expected numbers of chromosomes of each gene arrangement can be calculated from the frequencies of the respective arrangements in the totals for separate

TABLE 10

FREQUENCIES (IN PER CENT) OF THE GENE ARRANGEMENTS IN THE THIRD CHROMOSOME IN
POPULATIONS INHABITING WILDROSE AND LONE PINE CANYONS, CALIFORNIA

ST, Standard; AR, Arrowhead; CH, Chiricahua; TL, Tree Line; SC, Santa Cruz; MM,
Mammoth; OL, Olympic; n, number of chromosomes examined

Station	Date of collecting	ST	AR	CH	TL	SC	MM	OL	n
Wildrose A and B....	May 20, 1937	13.8	67.4	18.7	0	0	0	0	224
Wildrose A	May 26, 1938.....	34.0	37.8	25.0	0.6	1.9	0.6	0	156
	Oct. 2, 1938	31.1	41.9	18.9	5.4	2.7	0	0	74
	June 9, 1939.....	35.3	45.8	15.3	3.2	0.5	0	0	190
	May 30, 1940	24.5	43.4	26.4	5.7	0	0	0	106
Wildrose B	June 9, 1939	30.5	51.0	13.7	4.7	0	0	0	190
	May 30, 1940	27.0	56.0	16.0	0	0	1.0	0	100
Wildrose C	June 10, 1939....	37.0	49.0	13.0	1.0	0	0	0	100
	May 31, 1940	35.2	38.9	22.2	1.8	0	1.8	0	54
Wildrose D	June 10, 1939 .	52.0	34.0	12.0	2.0	0	0	0	100
	May 31, 1940	39.0	37.0	20.0	4.0	0	0	0	100
Lone Pine	July 1937	21.7	69.6	8.7	0	0	0	0	46
	July 1938	21.2	56.5	18.1	3.2	0	0	1.1	94
	July 1940	18.2	58.2	12.7	9.1	0	0	1.8	55

stations. The degree of uniformity of the samples at each station is then
expressed in terms of a χ^2 value. A difficulty is encountered with the rare
arrangements: for some of them the expected values are too low to permit
the calculation of a χ^2 with the aid of the usual method. Such rare arrange-
ments have accordingly been disregarded. The results of the calculations for
the collecting stations listed in table 10 are as follows (the 1937 sample being
disregarded):

Station	χ^2	Degrees of freedom	Probability
Wildrose A	13.324	9	0.20–0.10
Wildrose B	3.455	3	0.50–0.30
Wildrose C	0.922	2	0.70–0.50
Wildrose D	4.618	2	0.10–0.05
Lone Pine	4.772	4	0.50–0.30

No significant changes were observed at Wildrose from 1938 to 1940 and
at Lone Pine Canyon from 1937 to 1940. All the samples at these stations were,
with one exception, taken at the same season. In this respect the data for the
population of Aldrich, Texas are more satisfactory. Samples at that station
were collected by J. T. Patterson at frequent intervals during the seasons when
Drosophila pseudoobscura is reasonably abundant (spring and autumn), and
were sent to the writer for examination. Tables 1 and 11 summarize the data
obtained. It appears that the Arrowhead and Olympic arrangements were

less common in 1939 than they were in 1940 and 1941, whereas Pikes Peak and Estes Park were more common in 1939 than in 1940. Furthermore, both in 1939 and in 1940, Arrowhead was most common in March, decreased in frequency as the season advanced, and recovered during the winter period. Pikes Peak seemingly showed a seasonal trend which is the reverse of that displayed by Arrowhead. A χ^2 analysis has been made to test the reality of these changes. Grouping the data by months regardless of the year of collecting, χ^2 turns out to be 19.976. For 9 degrees of freedom, this or a greater value is expected to occur by chance in 1 or 2 per 100 trials. The seasonal change appears, therefore, to have been real. Combined data for 1939 and 1940 can now be compared (the sample for 1941 is disregarded because it was too small; Patterson informs the writer that in 1941 the species was rare at Aldrich). The χ^2 is 31.777, and is, for 4 degrees of freedom, very significant. The greatest con-

TABLE 11

FREQUENCIES (IN PER CENT) OF THE GENE ARRANGEMENTS IN THE THIRD CHROMOSOME IN POPULATIONS INHABITING ALDRICH (NEAR AUSTIN), TEXAS

AR, Arrowhead; PP, Pikes Peak; TL, Tree Line; OL, Olympic; EP, Estes Park; n, number of chromosomes examined

Date of collecting	AR	PP	TL	OL	EP	n
March 1939	19.5	74.4	5 5	0	0.6	164
April 1939	18.8	74.2	5.1	0.3	1.6	314
May 1939	11.24	83.1	4.5	0	1.1	89
Autumn 1939	5.8	82.7	11.5	0	0	52
March 1940	26.5	64.2	6.6	2.7	0	366
April 1940	23.7	66.2	7.5	1.8	0.9	228
May 1940	18.42	71.1	5.3	5.3	0	38
April 1941	3.6	82.1	7.1	7.1	0	28

tribution to this χ^2 is made by the Arrowhead and Olympic arrangements, the average frequencies of which were, therefore, different in the two years.

The data referred to above are instructive, but by far the most extensive data on temporal changes in the frequencies of gene arrangements have been secured at nine collecting stations grouped in three localities at Keen Camp, Piñon Flat, and Andreas Canyon, on Mount San Jacinto, California. A preliminary account of this work has already been published by Dobzhansky (1941c), and a more detailed account will be published elsewhere when the work has been completed. Only a general summary of the conclusions as they stand at present will be presented here, because of their importance to the general scheme of the present investigation.

By these data it is established that in at least two of the localities (Piñon Flat and Andreas Canyon) the gene arrangements show significant changes in frequency from month to month. Furthermore, the changes there appear to follow a seasonal cycle: Standard is commonest during the cool part of

the breeding season, and decreases in frequency as the weather becomes hot and dry. Chiricahua displays the converse cycle. But at Keen Camp, which is only about 15 miles from Piñon Flat and 10 miles from Andreas Canyon, the changes either do not occur at all or are less pronounced and less regular than in the other two localities.

So great an instability of the relative frequencies of gene arrangements demands an explanation. As a working hypothesis, it seems justifiable to assume at present that the species population is a mixture of genetic types of different ecological optima. The yearly cycle of seasonal climatic and other changes evokes an adaptive response in the species population; this response finds its expression in an increase in the frequencies of those genetic variants which have the highest adaptive value in the environment prevailing at a given period of the year, and a decrease in the frequencies of the temporarily less suitable variants. The changes in relative frequency are therefore produced by the pressure of natural selection; the signs and the absolute values of the selection coefficients are, however, themselves changing in accordance with the seasonal cycle of the climate.

A population change of an apparently similar nature has been observed in another insect, *Adalia bipunctata,* in which certain heritable color varieties increase in frequency during the summer breeding period but are partly eliminated during hibernation (Timofeeff-Ressovsky, 1940). But the reasons why the different gene arrangements in the third chromosome appear to differ in adaptive values at different seasons are as yet obscure; the most plausible view is that in certain populations genetic variants which determine the fitness of their carriers at different seasons have become, by chance, associated with certain gene arrangements. However that may be, it is clear enough that the composition of the populations of *Drosophila pseudoobscura* which inhabit some territories is in constant change not only in terms of an average human lifetime, but even in terms of much shorter time intervals. This fact is in itself of profound interest. Indeed, if evolution is to be defined as a change in the genetic composition of populations, evolutionary modifications are taking place before our eyes and are directly observable.

In the pursuit of racial studies, the inconstancy in time of the population genotype raises no small difficulty. A population sample, no matter how large, reflects the status of that population only at the time the sample is taken. The same population may assume a new aspect next year or even next month. It is therefore desirable to compare different populations either by sampling them all simultaneously, or, better still, by sampling each population repeatedly, at different seasons and over a period of years. For obvious reasons these desiderata are difficult to attain in practice. Hence, a large majority of localities in our material are represented each by a single sample collected on a single day at various times during the breeding seasons of the flies. Fortunately, the amplitude of the temporal fluctuations in the localities thus far studied in this respect is small as compared with the differences which have been found between the populations which inhabit different geographic regions.

POPULATION DIFFERENCES OF GEOGRAPHICALLY CLOSE LOCALITIES

The degree to which a species population is subdivided into genetically and territorially distinct units, that is, into geographic races, varies from organism to organism. The fineness of subdivision is usually assumed to stand in an inverse relation to the efficiency of the means of dispersal possessed by the organism in question. Forms that are able, actively or passively, to traverse long distances are genetically homogeneous over large territories; forms which at no stage of their life cycle move from place to place may differentiate in adjacent colonies. Land snails are the classic example of the extremely fine subdivision of species into local races. The recent work of Welch (1938) and of Diver (1939) has demonstrated that snail populations of stations a fraction of a mile apart (and in extreme cases only a few yards) may be distinguishable. In the desert plant *Linanthus parryae,* population samples taken at distances of 1½ miles or more apart show no correlation in their composition (Epling and Dobzhansky, 1942). Both active (by flight) and passive (e.g., by wind) transport over relatively long distances being possible in *Drosophila pseudoobscura,* at least in theory, the very fine geographic subdivision of the species population observed in that insect is unexpected.

Dobzhansky and Queal (1938) have compared samples collected on different mountain ranges in the Death Valley region of California and Nevada. The adjacent ranges are, on the average, about 50 miles apart, and the most remote ones about 200 miles apart. A single sample was taken on each range, from an area no greater than ½ mile in length. All the samples were taken within two months in the summer of 1937. Eight out of eleven samples showed significant differences in the relative frequency of some gene arrangements in the third chromosome. Koller (1939) has compared samples taken in different canyons of a single mountain range (Panamint) in the same region. The average distance between the adjacent canyons was less than 4 miles, and the most remote canyons were no more than 20 miles apart; populations of some of the canyons were significantly different from those of other canyons, and the magnitude of these differences proved to be only slightly smaller than that observed by Dobzhansky and Queal between populations of separate ranges. Comparison of population samples taken at stations between ½ and 1½ miles apart in southern Texas suggests that populations even so closely adjacent may be genetically distinct (Dobzhansky, 1939*b*).

The discovery, however, that the composition of a given limited population may vary with time (see above) makes it necessary to re-examine this problem of geographic differences in its light. The frequency of a gene arrangement in a population now appears to be a far more plastic character than was formerly supposed. If a species can respond to even the seasonal changes in its environment by altering the composition of its populations, the differences between the inhabitants of different collecting stations may be far less significant than was supposed, and may express merely the vagaries of the shifting equilibrium between the organism and its milieu. The problem is, there-

fore, twofold. In the first place, it is desirable to know what is the minimum distance which permits two populations to become at least temporarily different in genetic constitution. Second, the distance at which the differences between populations may exceed the amplitude of the temporal fluctuations should be determined.

The four collecting stations at Wildrose Canyon furnish some relevant data (table 10). The distances between these stations are, as stated above, between ⅓ mile (A to B, C to D) and 3 miles (B to D). The frequency of the Standard gene arrangement at Wildrose D in June 1939 was 52 per cent; at the same time it was only 30 per cent at Wildrose B. In May 1940, the Arrowhead chromosomes amounted to 56 per cent of the total at Wildrose B, and to only 37 per cent at D. To test the statistical significance of these differences, calculations were made for the four Wildrose stations for the years 1939 and 1940 separately and for both years combined. For this purpose the chromosomes were divided into three categories, namely Standard, Arrowhead, and the remaining arrangements (Chiricahua, Tree Line, Santa Cruz, and Mammoth) combined. The following results were obtained:

Year	χ^2	Degrees of freedom	Probability
1939	14.484	6	0.05–0.02
1940	13.774	6	0.05–0.02
1939–1940	20.960	6	<0.01

The differences between the populations of the Wildrose collecting stations are, therefore, significant. The available data do not permit us to decide how permanent these differences may be in time. No change in the composition of these populations was observed between 1939 and 1940, but the change observed between 1937 and 1938 within Wildrose stations A and B is as great as the differences between the stations themselves (see above).

Much more extensive data are available for the three localities, Keen Camp, Piñon Flat, and Andreas Canyon, on Mount San Jacinto, California. In the summers of 1939 and 1940 collections were made at approximately monthly intervals from April to September at five collecting stations at Keen Camp. Similar collections were made at two stations at Piñon Flat and two stations at Andreas Canyon. At a single station in each locality the periodic collecting was continued through 1941 and 1942. The stations at Keen Camp are from ½ mile to about 2 miles apart; the distances between the three localities themselves are from 10 to 15 miles (see Wright, Dobzhansky, and Hovanitz, 1942). A detailed account of these observations will be published later; a brief summary is presented in table 12.

In the summer of 1939 Standard chromosomes were more frequent at Keen Camp A and Keen Camp B stations (31.5 and 31.6 per cent) than at Keen Camp C, D, or E (22.5, 25.4, and 26.7 per cent respectively). On the contrary,

Chiricahua chromosomes were commoner at Keen Camp C, D, and E than at A and B (table 12). The frequencies of Arrowhead and Tree Line were uniform throughout the Keen Camp locality. A statistical test gives χ^2 equal to 24.227, which, for 12 degrees of freedom, may occur by chance only about twice in 100 trials. The differences are, therefore, fairly significant. The summer of 1939 was hot and dry; the fly populations declined in numbers during July and August, particularly at Keen Camp C, D, and E, which are somewhat more arid than the other collecting stations at that locality. The data for 1940 show little apparent difference beween the populations of the several

TABLE 12

FREQUENCIES (IN PER CENT) OF THE GENE ARRANGEMENTS IN THE THIRD CHROMOSOME IN POPULATIONS ON MOUNT SAN JACINTO, CALIFORNIA

ST, Standard; AR, Arrowhead; CH, Chiricahua; TL, Tree Line; SC, Santa Cruz; n, number of chromosomes examined

Locality and station	Period of collecting	ST	AR	CH	TL	SC	n
Keen Camp A.....Summer 1939....		31.5	30.8	33.0	4.7	0	445
	Summer 1940....	34.9	23.2	38.7	2.6	0.5	568
Keen Camp B.....Summer 1939....		31.6	26.3	38.4	3.8	0	453
	Summer 1940....	30.9	22.8	42.4	3.9	0	382
Keen Camp C.....Summer 1939....		22.5	31.2	43.5	2.8	0	400
	Summer 1940....	29.7	22.7	43.7	3.9	0	384
Keen Camp D.....Summer 1939....		25.4	32.4	38.1	4.1	0	370
	Summer 1940....	29.4	25.8	39.9	4.6	0.2	418
Keen Camp E.....Summer 1939....		26.7	32.1	39.3	1.9	0	318
	Summer 1940....	31.6	19.7	44.6	4.0	0.2	630
Keen Camp, total 1939–1942		30.6	25.8	39.8	3.7	0.1	5132
Piñon Flat, total 1939–1942		40.9	26.4	28.0	4.0	0.6	3021
Andreas Canyon, total 1939–1942....		57.9	24.5	14.6˙	2.6	0.4	3494
Mt. San Jacinto, total 1939–1942 ...		41.5	25.6	29.2	3.4	0.3	11647

stations; the χ^2 for 1940 is 13.778; for 12 degrees of freedom this has a probability of chance occurrence in from 30 to 50 out of 100 trials, hence the differences are not significant. The summers of 1940 and 1941 were more favorable for the flies than that of 1939. Small differences between the populations were also established between the two collecting stations at Piñon Flat in 1939. There, as well as at Keen Camp, the amplitude of the interstation differences within a locality was less than the amplitude of the temporal fluctuations in the frequencies of the gene arrangements.

The populations of the Keen Camp, Piñon Flat, and Andreas Canyon localities taken as wholes can now be compared. The lower part of table 12 gives the pertinent data, that is, the frequencies of the several gene arrangements in the entire material from these localities. Standard was appreciably

commoner at Andreas Canyon than at Keen Camp (57.9 and 30.6 per cent respectively), whereas Chiricahua reached its highest frequency at Keen Camp and its lowest at Andreas Canyon (39.8 and 14.6 per cent). The frequency of Arrowhead was about the same in the three localities. The Piñon Flat population was about intermediate between those inhabiting Keen Camp and Andreas Canyon. The differences are obviously significant: the χ^2 for 6 degrees of freedom is 843.057, which has only an infinitesimal probability of being due to chance. More important still, the differences observed between the localities are outside the range of the temporal fluctuations observed in the populations which inhabited these localities during the period from 1939 to 1941. It appears, therefore, that, despite seasonal fluctuations, populations residing 10 to 15 miles apart may show permanent differences in the frequencies of the gene arrangements of the third chromosome.

It is to be noted that the entire territory between Keen Camp, Piñon Flat, and Andreas Canyon is habitable by the flies and contains no obvious impediments to their migration. On the other hand, because of great differences in elevation and topography, the environments in the three localities are very dissimilar. Keen Camp, in the yellow pine forest, has a relatively mild summer and a severe winter, with snow; at Andreas Canyon, on the margin of the Colorado Desert, the winters are mild and are the most favorable season for the breeding of the flies, the summers being extremely hot and dry; Piñon Flat, in the pine-juniper woodland, is intermediate (see Wright, Dobzhansky, and Hovanitz, 1942). It is tempting to suppose that the differences in the frequencies observed in the populations of these three localities are somehow correlated with the prevailing climatic or other environmental differences. The seasonal cyclic alterations in the frequencies of Standard and Chiricahua arrangements observed at Andreas Canyon and at Piñon Flat seem to indicate that such a correlation may well be present. A closer analysis of the data, however, leads to apparently contradictory results: Standard is commoner at Andreas Canyon and at Piñon Flat during the cool season, and relatively rare during the hot months; hence one would expect to find it most common in the locality which has the lowest mean yearly temperature, namely Keen Camp, and least frequent in the warmest locality, namely Andreas Canyon. The actual situation is just the reverse: Standard is commonest at Andreas Canyon and least common at Keen Camp. Chiricahua is seasonally commonest during the hot months, yet it is most frequent at Keen Camp, which is the coolest locality. This situation will be analyzed further in another publication; for the time being it is sufficient to state that the most likely solution of the above contradiction is that the adaptive values of the gene arrangements are determined not by the gene order as such (i.e., not by position effects), but by gene variants (mutant genes) which happen to be associated with the given gene arrangement in different localities.

Analysis of the frequency of the "sex ratio" in the Mount San Jacinto populations leads to essentially the same conclusions. As was shown above (p. 97), the populations of Keen Camp, Andreas Canyon, and Piñon Flat differ sig-

nificantly in the frequencies of the "sex ratio," Keen Camp having the highest, Piñon Flat the lowest, and Andreas Canyon an intermediate frequency. No differences have been observed, however, between the populations of the five collecting stations at Keen Camp either in 1939 or in 1940. The χ^2's for these collecting stations are: for 1939, 2.276; for 1940, 6.631; and for the period 1939-1941, 5.412. For 4 degrees of freedom such or greater values may occur by chance frequently enough to make them statistically insignificant.

A proof of the genetic difference of populations which inhabit stations a fraction of a mile to 2 miles apart, completely independent of the above, is afforded by analysis of the frequency of allelism of the concealed lethal mutant genes found in the third chromosomes (Dobzhansky and Wright, 1941; Wright, Dobzhansky, and Hovanitz, 1942). It has been shown that the lethals found in the population of a given station on Mount San Jacinto or in the Death Valley region are alleles more frequently than the lethals found in the populations of different stations in the same locality. Similarly, the lethals found within a locality are alleles more frequently than those found in different localities.

We are led, therefore, to the conclusion that populations of *Drosophila pseudoobscura* are in fact relatively sedentary, and that transport over appreciable distances, whether active or passive, is negligible.

Geographic Gradients in Drosophila pseudoobscura

It is now well established that individuals which compose the population of a given territory frequently differ from one another in the gene arrangements of their chromosomes. Some individuals are structural homozygotes and others structural heterozygotes. Some carry a gene arrangement in one or in both chromosomes of a pair which is not present in the homologous chromosomes of other individuals in the same population. Nevertheless, taken collectively, the population of a given territory is characterized by the relative frequencies of its different gene arrangements. But the composition of the populations of some territories does not remain static in time. Changes, apparently of a cyclic nature, may take place from month to month. Notwithstanding these changes, the populations of localities as little as 10 miles apart may differ permanently in the relative frequency of different gene arrangements and of other genetic characters.

The question now arises whether these permanently different populations show any regularities in geographic distribution. One of the simplest regularities is a correlation between the composition of populations of different localities on the one hand, and the distance which separates these localities on the other. The experience of systematists in various groups of organisms shows that as one moves from place to place in a given direction, the inhabitants of the country traversed frequently change more or less gradually. The inhabitants of remote localities and regions tend to differ more than those of neighboring localities. This is the phenomenon of geographic gradients, or, as Huxley

(1938) has proposed to call them, clines. If clines in the distribution of an organism are discovered, it is necessary to consider whether the gradient they show is caused by directive influences of the environment or by historical causes, such as the paths of migration which the species might have taken during its spread from the territory of its origin, or the vicissitudes of its existence in geological history.

The alternative to clinal variation is a variation that is geographically haphazard. The composition of populations of different localities may stand in no relation to the distance between these localities. Again, situations intermediate between the clinal and the haphazard distribution may be encountered. A species may respond to the pressure of the environment by forming local variants which are adapted to the conditions which prevail in each type of habitat encountered in its general distribution area. Since many types of habitat (forests, swamps, sand dunes, mountain slopes with southern or northern exposure, etc.) frequently recur mosaic fashion in geographically extensive regions, the characteristics of a population may to all appearances change irregularly along a given transect, and yet may be very definitely tied to the microenvironment. Such variants, recurring wherever a certain type of habitat is encountered in the distribution area of a species, are termed ecotypes (Turesson, 1922). It is reasonable to suppose that the clinal, the ecotypic, and the geographically haphazard distributions may be more or less superimposed one upon another. The habitats of a given class may become less and less frequent as one passes from one part of the country into another, and the ecotype adapted to that habitat may become correspondingly less and less common. On the other hand, an ecotype may become a geographic race which continuously occupies a large expanse of territory. Geographically haphazard variation, because of restriction of the genetically effective population size, may result in the formation of superior adaptive types which may spread and occupy extensive territories or common types of habitat.

Population samples from various parts of the distribution area of *Drosophila pseudoobscura* and *D. persimilis* have been examined for the gene arrangements in their chromosomes. The resulting data (tables 1–5) permit a general review of the populations of the species. On account of temporal variations in the composition of populations, such a review would, ideally, require that each section of the species area be sampled in many localities and at different seasons over a period of years. The material available is evidently far removed from this ideal. Nevertheless, it is believed that even the data as they now stand are sufficient to give some insight into the real situation. The conditions in *D. pseudoobscura* will be considered first, *D. persimilis* being discussed thereafter. The gene arrangements in the third chromosome furnish the most interesting data. The gene arrangements in the XR chromosome have been discussed above, and will be referred to in the present section only briefly.

The territory along the United States–Mexican border has been sampled fairly adequately. This territory forms a transect across the distribution region of *D. pseudoobscura* in a general west-east (more precisely, from west-northwest

to east-southeast) direction. The frequencies of the gene arrangements commonly found in this territory are given in table 13 and are graphically represented in figure 10. This and the following figures were constructed as follows: The horizontal rows indicate the frequencies of a given gene arrangement (the name of which appears on the left) in different localities or groups of localities. The vertical rows show the frequencies of different gene arrangements in the same locality. The circles on the map in the upper part of the diagram denote the approximate position of the localities in question, the circles being connected by dotted lines with the black columns, the height of which is proportional to the relative frequencies of the respective gene arrangements in the populations concerned. The scales on the left and right indicate percentages.

Table 13 and figure 10 show that, in the region along the Mexican border, the frequency of the Standard gene arrangement decreases from west to east. It becomes rare in Arizona, but does not disappear entirely even in Texas. Arrowhead reaches very high frequencies in Arizona and New Mexico, and declines both to the east and to the west. The data show very regular gradients for Arrowhead, with one exception: the sample from the Huachuca Mountains in Arizona had fewer Arrowhead chromosomes than that from Prescott. This exception is probably accounted for by the position of the two regions: Prescott lies considerably to the north of Tucson and the Huachuca Mountains, and, in Arizona, the frequency of the Arrowhead arrangement declines from north to south. Pikes Peak shows a beautiful gradient: it does not occur in California, is rare in Arizona, becomes common in New Mexico, and is the predominant arrangement in the Texan populations. Santa Cruz (not shown in figure 10) is relatively common on the Pacific coast, but disappears rapidly as one moves eastward. Chiricahua appears to be commoner in the mountains of California than it is along the Pacific coast; the frequency of this arrangement declines from California eastward, and it is not found in Texas except in the westernmost part of that state, in the Trans-Pecos area. The regularity of the gradient for Chiricahua is broken by the high value observed in the Huachuca Mountains. The significance of this fact is clear: Chiricahua is the predominant gene arrangement in the state of Chihuahua, Mexico, and the Huachuca Mountains harbor the northernmost outpost of the Mexican distribution center of this arrangement. Tree Line and Olympic occur on the two ends of our transect (in California and in Texas) but are rare or absent in the middle (in Arizona and in New Mexico). Tree Line shows gradients, decreasing in frequency eastward from California, and increasing from Arizona eastward to Texas.

A second west-east transect across the distribution area of *D. pseudoobscura* was made at a latitude approximately 300 miles north of the first, that is, through middle California, southern Nevada, northern Arizona and southern Utah, northern New Mexico and southern Colorado, and the more northerly part of Texas. The results are summarized in table 14 and figure 11. The regularities observed in this transect are similar to those of the first transect;

TABLE 13

ST, Standard; AR, Arrowhead; CH, Chiricahua; TL, Tree Line; SC, Santa Cruz; OL,
Olympic; n, number of chromosomes examined

Region	ST	AR	PP	SC	CH	TL	OL	n
San Rafael Mts. and Santa Barbara, Calif.	47.5	20.8	0	7.8	16.2	7.3	0.5	438
Santa Monica, Pasadena, and San Gabriel, Calif.	54.1	19.8	0	1.7	17.8	6.6	0	303
Mt. San Jacinto, Calif.	41.5	25.6	0	0.3	29.2	3.4	0	11647
Mojave and Colorado deserts, Calif.	15.4	73.2	0	0.3	10.0	1.0	0	370
Prescott, Ariz.	11.0	79.0	1.0	0	9.0	0	0	100
Tucson, Huachuca, and Sonoita, Ariz.	4.1	66.4	4.1	0	25.4	0	0	122
Cochise County, Ariz.	0.5	88.5	4.2	0	6.3	0.5	0	192
Grant County, New Mex.	0	91.9	4.7	0	2.7	0.7	0	148
Doña Ana and Lincoln counties, New Mex.	0.4	69.1	24.2	0	5.1	1.2	0	256
Trans-Pecos area, Tex.	0.9	27.4	65.6	0.	2.4	3.3	0	212
South-central Tex.	0.2	11.7	70.3	0	0	12.4	5.3	418
Valley area, Tex.	0	3.3	76.7	0	0	16.7	3.3	30

TABLE 14

Abbreviations as in table 13

Region	ST	AR	PP	SC	CH	TL	OL	n
Santa Lucia Mts., Calif.	51.0	21.0	0	14.0	11.0	2.0	1.0	100
Southern Sierra Nevada, Calif.	28.3	51.8	0.3	0.6	11.6	5.1	2.4	338
Death Valley region, Calif., western part	30.8	50.1	0	0.3	16.9	1.7	0	3328
Death Valley region, Calif. and Nev., eastern part	20.6	67.5	0	0	12.0	0	0	894
Grand Canyon, Ariz.	0.5	97.0	0	0	2.5	0	0	200
Flagstaff and Black Mesa, Ariz.	2.4	95.8	1.2	0	0.6	0	0	168
Mesa Verde, Colo.	0	100.0	0	0	0	0	0	100
Raton Mesa, New Mex.	0	80.0	18.2	0	0.9	0.9	0	110
Plains area, Tex.	0	26.1	70.6	0	0	2.2	0	92
North-central Tex.	0	21.5	70.2	0	0	6.1	1.4	1315
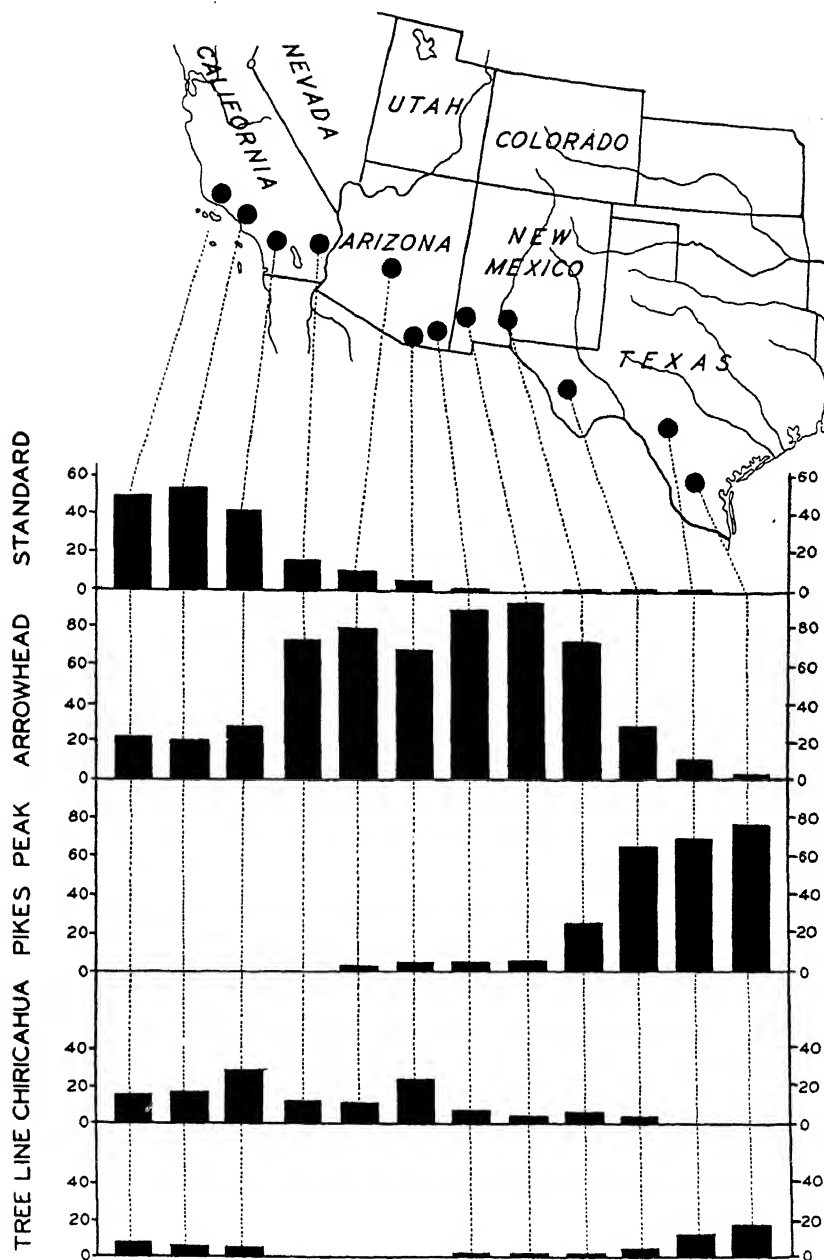
FIG. 10. West-east transect across the distribution area of *Drosophila pseudoobscura*, along the United States–Mexican border. The heights of the black columns symbolize the relative frequencies of the third-chromosome gene arrangements the names of which appear on the left. The numerals indicate percentages of the respective gene arrangements in the populations. The black spots on the map show the geographic origin of the population samples.
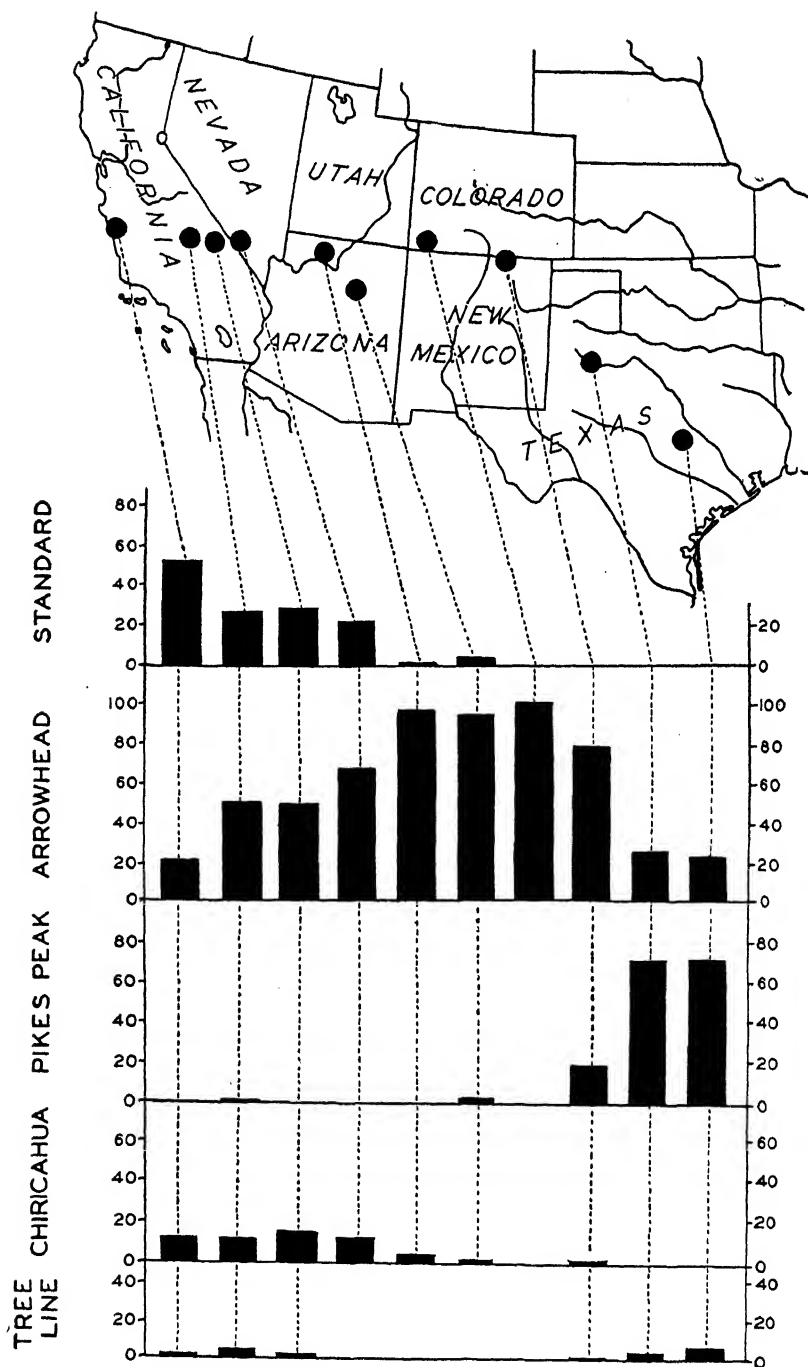
Fig. 11. West-east transect across the distribution area of *Drosophila pseudoobscura*, about 300 miles north of that shown in figure 10. For further explanation see figure 10 and text.

the data are nicely complementary. The Standard arrangement is commonest on the Pacific coast, diminishes in frequency eastward, and disappears in New Mexico and Colorado. Arrowhead shows an ascending gradient from the Pacific coast eastward, reaches 100 per cent frequency at Mesa Verde, and forms a descending gradient toward the eastern limit of the species area in Texas. Santa Cruz and Chiricahua decrease in frequency eastward and Pikes Peak westward; Tree Line and Olympic occur at the ends of the transect but not in the middle. No major irregularities are observed in the entire material.

If one compares the two transects thus far described (tables 13 and 14, figs. 10 and 11), the similarities of the populations found at approximately the same longitude on both transects stand out most conspicuously. Minor differences are present, however, and these differences suggest the existence of north-south gradients. For example, Arrowhead is more frequent in the southern Sierra

TABLE 15

FREQUENCIES (IN PER CENT) OF GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF *Drosophila pseudoobscura*. WEST-EAST TRANSECT AT ABOUT 38°–42° NORTH LATITUDE

Abbreviations as in table 13

Region	ST	AR	PP	SC	CH	TL	OL	n
Northern Coast Ranges, Calif.	37.8	33.9	0.7	12.8	5.3	7.7	1.5	413
Northern Sierra Nevada, Calif.	28.0	44.2	0	7.0	6.7	8.8	5.2	328
Toyabe Range, Nev.	6.3	81.2	0	0	12.5	0	0	16
Salt Lake City and Uinta Mts., Utah	0	96.7	3.3	0	0	0	0	30
Rocky Mountains from Estes Park to Pikes Peak, Colo.	4.4	36.0	44.9	0	0	3.7	2.2	36

Nevada than in the Santa Monica–Pasadena–San Gabriel region, at the Grand Canyon than in the Huachuca Mountains, at Mesa Verde than in Grant County of New Mexico, at Raton Mesa than in Doña Ana and Lincoln counties of New Mexico or the Trans-Pecos area of Texas, and in north-central Texas than in the south-central and Valley areas of Texas. Each pair of territories named above lie at about the same longitude but at different latitudes. The frequency of Arrowhead decreases, therefore, from north to south. On the contrary, the frequencies of Pikes Peak, Chiricahua, and perhaps also of Tree Line tend to be higher in the southern than in the northern localities lying on about the same meridian. This is indeed confirmed by the samples from Chihuahua, Mexico; in these samples Chiricahua is the predominant gene arrangement, Pikes Peak is common, Arrowhead rare, and Standard absent.

Except for California, the territory which lies north of the second transect described above has been sampled very inadequately. Table 15 presents the scanty data which, taken as a group, form a third west-east transect between the latitudes 38° and 42°. As far as they go, these data confirm the existence

of the gradients discussed above. The Standard arrangement decreases in frequency from west to east, but the material is insufficient to indicate whether it occurs in northern Utah as well as in the central part of the Rocky Mountains of Colorado, or whether it is absent from Utah. As the data stand, the gradient is irregular. The Arrowhead arrangement forms a gradient sloping down both westward and eastward from the center. Tree Line and Olympic are again found at the ends of the transect but not in the middle; Santa Cruz is confined to the Pacific coast, and Chiricahua, which is less common at this latitude than farther south, shows the highest frequency in the very small sample from central Nevada.

TABLE 16

FREQUENCIES (IN PER CENT) OF GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF
Drosophila pseudoobscura. THE PACIFIC COAST POPULATIONS

Abbreviations as in table 13

Region	ST	AR	PP	SC	CH	TL	OL	n
Friday Harbor, Seattle, and Willapa Bay, Wash.	53 5	10 5	4.6	0	19 8	10 4	1.2	86
Selma, Ore.	18 8	53 1	0	1.6	18 8	7.8	0	64
Mendocino, Calif.	52.9	35.7	0	1.4	10.0	0	0	70
Guerneville, Sebastopol, and Cotati, Calif.	43 8	12 8	2.1	36.5	0	5.2	0	96
Monterey, Calif.	54 7	12 5	0	20 3	7.8	0	4.7	64
Santa Lucia Mts., Calif.	51.0	20.2	0	13.5	12.5	1.9	1.0	104
San Rafael Mts. and Santa Barbara, Calif.	47.5	20.8	0	7.8	16.2	7.3	0.5	438
Santa Cruz and Santa Rosa Islands, Calif.	45.9	13.9	0	30.9	7.7	1.5	0	194
Santa Monica, Pasadena, and San Gabriel, Calif.	54.1	19.8	0	1.7	17.8	6.6	0	303
Santo Tomas and San Antonio Mesa, Baja Calif.	58 7	25 0	0	2 9	13 5	0	0	104
Cedros Island, Baja Calif.	53 8	30 8	0	15 4	0	0	0	26

Transects which run from north to south across the distribution area of *D. pseudoobscura* can now be considered. Table 16 and figure 12 summarize the data on the populations which inhabit the Pacific coast and the Coast Ranges from the state of Washington to Baja California. Examination of these data discloses a situation very different from that encountered on the west-east transects discussed above, namely, absence of pronounced geographic gradients. For example, the frequency of Standard is very nearly the same everywhere, except in the Selma, Oregon sample. Selma, however, lies to the east of the Coast Ranges, and it may be questioned whether it belongs on this transect. The frequency of Arrowhead varies irregularly. Santa Cruz is commoner in California than in the north, and commoner on the islands than it
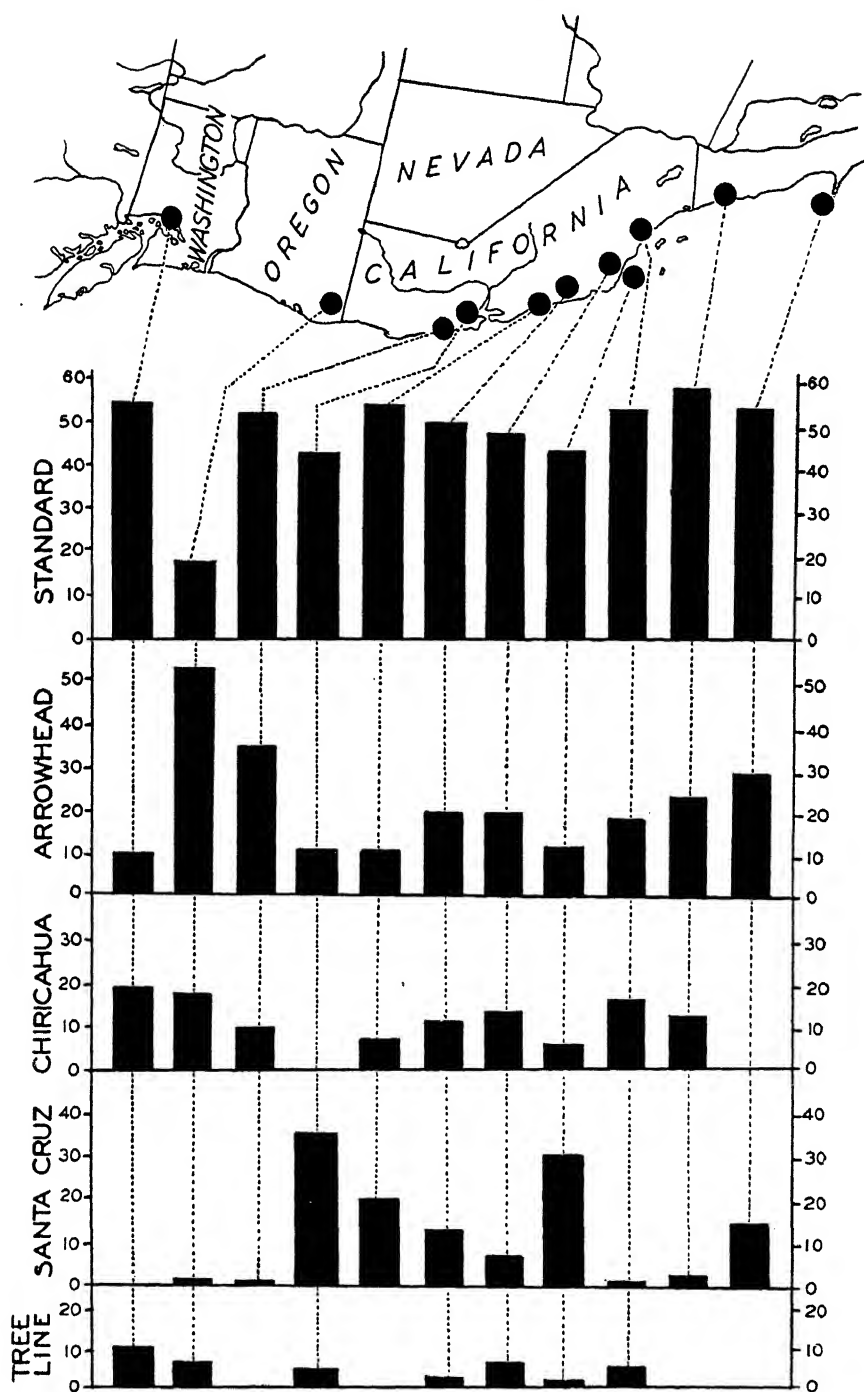
FIG. 12. Populations of *Drosophila pseudoobscura* inhabiting the Pacific coast. For further explanation see figure 10 and text.

is on the mainland. The distributions of Chiricahua and Tree Line show no regularity.

Another north-south transect can be made along the general course of the Cascade Range, the Sierra Nevada, and the mountains of southern California (table 17 and fig. 13). No geographic gradients are apparent on this transect either. Standard seems to be commoner in the north and in the south, where the transect approaches the ocean, than in the middle part, where the transect runs farther inland. Santa Cruz, Tree Line, and Olympic are relatively more common in the Sierra Nevada than they are in the Cascades or in transmontane southern California. Other arrangements vary quite irregularly. Sufficient material for north-south transects in the territory lying between the Cascade–Sierra Nevada and the Rocky Mountain systems is not available, except in its

TABLE 17

FREQUENCIES (IN PER CENT) OF GENE ARRANGEMENTS IN THE THIRD CHROMOSOME OF
Drosophila pseudoobscura. NORTH-SOUTH TRANSECT IN THE REGION OF THE
CASCADE AND SIERRA NEVADA RANGES

Abbreviations as in table 13

Region	ST	AR	PP	SC	CH	TL	OL	n
Princeton and Hope, B. C....	36.7	46.7	3.3	0	10.0	3.3	0	30
Methow, Wash.	52.0	47.0	0	0	1.0	0	0	100
Spray and Whitman, Ore....	25.9	55.6	3.7	0	11.1	1.9	1.9	108
Deer Creek, Calif..........	28.6	60.6	0	0.9	3.6	3.6	2.7	112
Placerville and Tahoe, Calif..	23.9	29.2	0	15.4	8.5	13.1	10.0	130
Mariposa, Calif.	37.5	38.9	0	2.8	9.7	9.7	1.4	72
Southern Sierra Nevada, Calif.	28.3	51.8	0.3	0.6	11.6	5.1	2.4	338
Mt. San Jacinto, Calif.......	41.5	25.6	0	0.3	29.2	3.4	0	11647
Borego, Banner, and Julian, Calif.	53.8	30.3	0	2.3	13.6	0	0	132

southern part. Comparison of the three west-east transects through that region (tables 13–15, figs. 10, 11) and the data for the state of Chihuahua, Mexico show that the frequency of Chiricahua decreases northward from the United States–Mexican border; Tree Line seems to behave like Chiricahua; Arrowhead increases in frequency northward. The data for the Rocky Mountain System itself are somewhat better. Table 18 shows a northwest-southeast transect through Colorado, New Mexico, western Texas, and Sierra Madre Oriental of Mexico.

In the Rocky Mountains, the highest frequency of Arrowhead has been observed in the sample from Raton Mesa, New Mexico (table 18). This arrangement becomes less frequent in southern New Mexico and in western Texas, and rare in Nuevo León, and is not known to occur at all in central and southern Mexico or in Guatemala. The behavior of Pikes Peak on this transect appears to be irregular. It is common in Colorado and in western Texas, relatively rare in the southern Rockies of New Mexico, rare in Nuevo León, common in
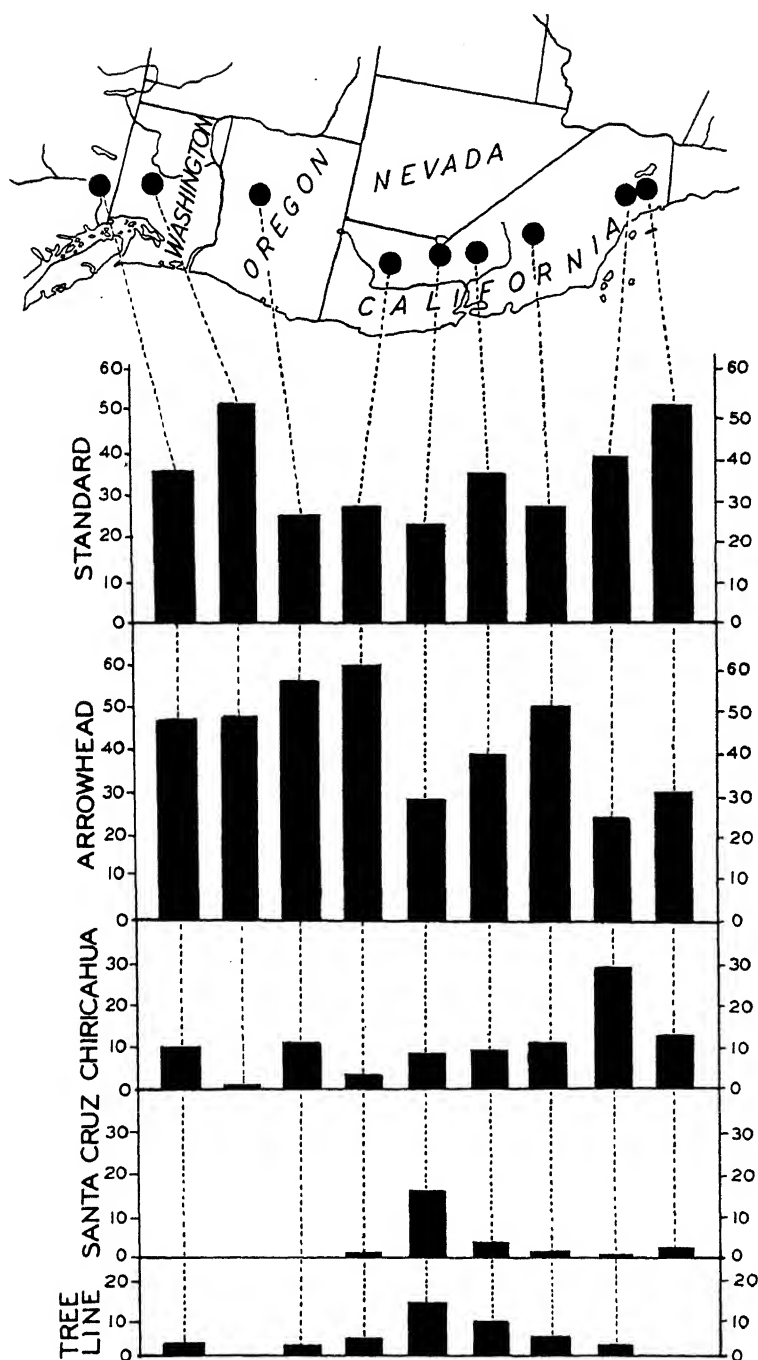
FIG. 13. North-south transect across the distribution area of *Drosophila pseudoobscura*, in the region of the Cascade and Sierra Nevada ranges. For further explanation see figure 10 and text.

Chihuahua, and found only sporadically in central Mexico. The high frequency of Pikes Peak observed in western Texas is not accidental, since it is known to reach very high frequencies in the central part of this state (cf. table 13). The Rockies of New Mexico evidently have a population which is modified by the influences emanating from the west: the high frequency of Arrowhead and the relatively low frequencies of Pikes Peak and Tree Line at Raton and in Doña Ana and Lincoln counties are reminiscent of the Arizonan populations. Tree Line and Olympic reach the highest frequencies known for these gene arrangements in Nuevo León, and rapidly decline northward; they are not very common in southern Texas (Valley area, table 13), rather rare in the southern Rockies, and apparently somewhat commoner again in the Rockies of Colorado. Populations of central and southern Mexico, as far

TABLE 18

Frequencies (in per cent) of gene arrangements in the third chromosome of *Drosophila pseudoobscura*. North-south transect through the Rocky Mountains and the Sierra Madre Oriental of Mexico

EP, Estes Park; other abbreviations as in table 13

Region	ST	AR	PP	CH	TL	OL	EP	n
Estes Park, Mt. Campbell, and Pikes Peak, Colo..........	4.4	36.0	44.8	0	3.7	2.2	3.8	136
Raton Mesa, New Mex.......	0	78.0	20.0 ·	1.0	1.0	0	0	100
Doña Ana and Lincoln counties, New Mex..........	0.4	69.1	24.2	5.1	1.2	0	0	256
Trans-Pecos area, Tex........	0.9	27.4	65.6	2.4	3.3	0	0	212
Saltillo and San Josecito, Nuevo León, Mex........	0	1.8	16.7	0	38.9	35.2	5.6	54
Pachuca, Hidalgo, Mex......	0	0	0	0	30.0	15.5	2.2	90

north as Hidalgo, are characterized by high frequencies of the Cuernavaca arrangement (not shown in table 18). This arrangement is not known either in Texas, in Nuevo León, or in Chihuahua. The boundary between populations of the Mexican and the Texan types is probably rather sharp, but its location is unknown. The populations of Nuevo León are intermediate only in the sense that they contain more Pikes Peak than the Mexican but less than the Texan ones; otherwise they are quite different from either. The same is true of the population of Chihuahua: here Chiricahua is predominant, Pikes Peak common, Olympic and Tree Line rather rare, and Arrowhead reaches its known southern limit.

The study of geographic gradients has shown that, with some exceptions, the composition of populations becomes more and more different as the distance separating them in space increases. The gradients are steeper in some regions, gentler in others, but the rule generally holds. As to the exceptions, the absence of clear-cut gradients on the two north-south transects along

the Pacific coast and the Sierra-Cascade ranges (tables 16, 17, figs. 12, 13) is most striking. An insight into the nature of these exceptions may perhaps be gained if we arrange the populations not according to arbitrary transects, but according to the nature and the geologic origin of the country which they inhabit. A subdivision of the western United States into physiographic provinces has been proposed by Fenneman (1911). Table 19 shows our data grouped according to these provinces.

The Pacific Border and Sierra-Cascade provinces, which embrace the whole territory between the Pacific Ocean and the Sierra-Cascade mountain chains, are characterized by high frequencies of Standard and Chiricahua, by presence of Santa Cruz and Tree Line, and by relatively low frequencies of Arrowhead.

TABLE 19

POPULATIONS OF *Drosophila pseudoobscura* CLASSIFIED ACCORDING TO FENNEMAN'S
PHYSIOGRAPHIC PROVINCES

Abbreviations as in tables 13 to 18. Frequencies in per cent

Province	Fenneman's designation	ST	AR	PP	SC	CH	TL	OL	EP	n
Pacific Border	24a, b, c, d	34.7	40.8	1.9	0.5	14.1	7.5	0.5	0	213
Pacific Border	24f	45.5	23.7	0.5	13.9	8.4	6.1	2.0	0	611
Pacific Border	24g	42.0	25.3	0	0.6	28.4	3.6	0	0	12427
Sierra-Cascades	23c, d	28.5	47.4	0.2	3.8	9.4	6.9	3.8	0	650
Columbia Plateau	22a, c	38.5	51.4	1.9	0	6.2	1.0	0	0	208
Basin and Range.	22a	27.4	55.5	0	0.2	15.3	1.4	0	0	4620
Basin and Range.	22b, d, e	2.5	68.3	20.7	0	7.2	1.1	0	0.1	1070
Colorado Plateau	21	1.2	97.0	0.4	0	1.4	0	0	0	568
Middle Rocky Mts.	18	0	96.9	3.1	0	0	0	0	0	32
Southern Rocky Mts. . . .	16	2.5	53.9	34.3	0	0.4	2.5	1.3	5.1	236
Great Plains	13k, i, 12f	0	26.1	70.6	-0	0	2.2	0	1.1	92
Coastal Plain	3f	0.1	18.9	70.4	0	0	7.8	2.2	0.7	1762

The middle part of the Pacific Border province (24f, including the California Coast Ranges from Mendocino County to Santa Barbara County) has a high frequency of Santa Cruz and a relatively low frequency of Chiricahua. The northern part of the same province (the coastal parts of Washington, Oregon, and northernmost California) and the Sierra-Cascade province have relatively high frequencies of Arrowhead. The Basin and Range province differs from the Pacific Border and Sierra-Cascade by still higher frequencies of Arrowhead and by absence or scarcity of Santa Cruz and of Tree Line and its derivatives (the only Santa Cruz chromosomes in this province have been found in the mountains of the Death Valley region, in proximity to the Sierra Nevada). The southern subdivisions of the Basin and Range province (southern Arizona and New Mexico) differ from its more northerly parts in the appearance of considerable numbers of Pikes Peak chromosomes and in dwindling frequencies of Standard. The populations of the Colorado Plateau province are most homo-

geneous of all; in some localities only Arrowhead chromosomes are present, and other gene arrangements occur in the province only as admixtures diffusing from the neighboring provinces. According to Fenneman's terminology, the Middle Rocky Mountains province includes northern Utah, western Wyoming, and eastern Idaho. Very little is known about the populations of this province, but the scanty data available suggest that it is similar to the Colorado Plateau. The Southern Rocky Mountains province (mountains of Colorado and northern New Mexico) is quite distinct from the preceding ones; Pikes Peak is common, the frequency of Arrowhead decreases, Tree Line and its derivatives are present although not very common, and Santa Cruz and its derivatives are almost wholly absent. The same situation obtains on the eastern margin of the distribution area of the species, in Texas, which falls into the Great Plains and the Coastal Plain provinces, where Arrowhead is even less common than in the Southern Rocky Mountains province, and Pikes Peak becomes the dominant constituent of the populations. By consulting tables 13 to 19 and figures 10 to 13 the reader can see that the transects which cross the boundaries of the physiographic provinces tend to show clear geographic gradients, whereas transects within a province generally do not. In particular, the two north-south transects along the Pacific coast and the Sierras (tables 16, 17, figs. 12, 13) lie within the Pacific Border and the Sierra-Cascade provinces and show no gradients.

The material from Mexico and Guatemala is too scanty to justify its subdivision according to physiographic provinces. Taken as a whole, these populations are characterized by predominance of Cuernavaca and of other Santa Cruz and Tree Line derivatives, and by absence or scarcity of Standard and its derivatives. The species *D. pseudoobscura* is, accordingly, differentiated into four major subdivisions. The first occupies the Pacific Border and Sierra-Cascade provinces; here Standard and Arrowhead are about equally abundant, followed by Chiricahua, Santa Cruz, Tree Line, and Olympic. The second embraces the Basin and Range, Colorado Plateau, and probably also the Northern and Middle Rocky Mountains provinces; Arrowhead is predominant, followed by Standard in the north and west and by Chiricahua and Pikes Peak in the south and east. The third subdivision covers the territory from the state of Colorado to Texas; the dominant arrangements are Pikes Peak and Arrowhead, followed by Tree Line and its derivatives. The fourth subdivision is in Mexico and Guatemala; the populations consist almost entirely of Santa Cruz and Tree Line with their derivatives.

GEOGRAPHIC GRADIENTS IN DROSOPHILA PERSIMILIS

The distribution area of *Drosophila persimilis* lies almost entirely within the Pacific Border and the Sierra-Cascade provinces of Fenneman. In contrast with *D. pseudoobscura,* the populations of *D. persimilis* have undergone a clear differentiation within this relatively limited area. Table 20 and figure 14 show a north-south transect along the Pacific coast (the Pacific Border province).

The northern populations, in Washington and Oregon, are almost pure Klamath, with admixtures of Cowichan, Mendocino, and Standard arrangements. The frequencies of Standard and Mendocino increase, though erratically, southward, the latter arrangement becoming predominant in at least some of the populations inhabiting the coast of California. The Whitney and Sequoia arrangements are rare, and have been found only in California.

TABLE 20

NORTH-SOUTH TRANSECT THROUGH THE DISTRIBUTION AREA OF *Drosophila persimilis* ALONG THE PACIFIC COAST

ST, Standard; SE, Sequoia; MD, Mendocino; KL, Klamath; CO, Cowichan; WH, Whitney; n, number of chromosomes examined. Frequencies in per cent

Region	ST	SE	MD	KL	CO	WH	n
Willapa Bay, Wash.	0	0	0	98.8	1.2	0	86
Cape Perpetua, Ore.	0	0	3.9	94.1	2.0	0	102
Selma, Ore.	4.0	0	10.0	86.0	0	0	50
Coffee Creek, Calif.	18.4	0	.7.9	68.4	2.6	2.6	38
Orick, Calif.	0.9	0.9	53.7	43.3	0	0.9	106
Weott, Calif.	12.1	0	29.3	58.6	0	0	58
Yollo Bolly, Calif.	20.8	0	13.9	59.7	0	5.6	72
Mendocino, Calif.	7.1	0.9	69.6	21.4	0	0.9	112
Ukiah to Monterey, Calif.	22.5	0	22.5	55.0	0	0	40

TABLE 21

NORTH-SOUTH TRANSECT THROUGH THE DISTRIBUTION AREA OF *Drosophila persimilis* ALONG THE CASCADE–SIERRA NEVADA CHAIN

Abbreviations as in table 20

Region	ST	SE	MD	KL	CO	WH	n
Hope and Princeton, B. C.	0	0	0	91.7	4.2	4.2	24
Seattle, Wash.	0	0	0	100.0	0	0	100
Whitman Forest, Ore.	12.5	0	0	75.0	0	12.5	8
Deer Creek, Calif.	7.1	0	7.1	57.1	0	28.6	14
Mariposa Grove, Calif.	30.0	0	0	10.0	0	60.0	10
Sequoia Park, Calif.	33.3	0.2	1.2	3.3	0	61.7	420
Coso Range, Calif.	30.0	0	0	0	0	70.0	20

Table 21 and figure 15 show another north-south transect leading along the Cascade and Sierra Nevada mountain chains. Despite the very small numbers of chromosomes in some of the samples, the situation is clear enough. As on the transect considered previously, the northern populations display a definite predominance of the Klamath arrangement and an admixture of Cowichan and Whitney. Farther south, Klamath becomes less frequent, and is replaced by Standard and Whitney. The last-named arrangement is predominant at
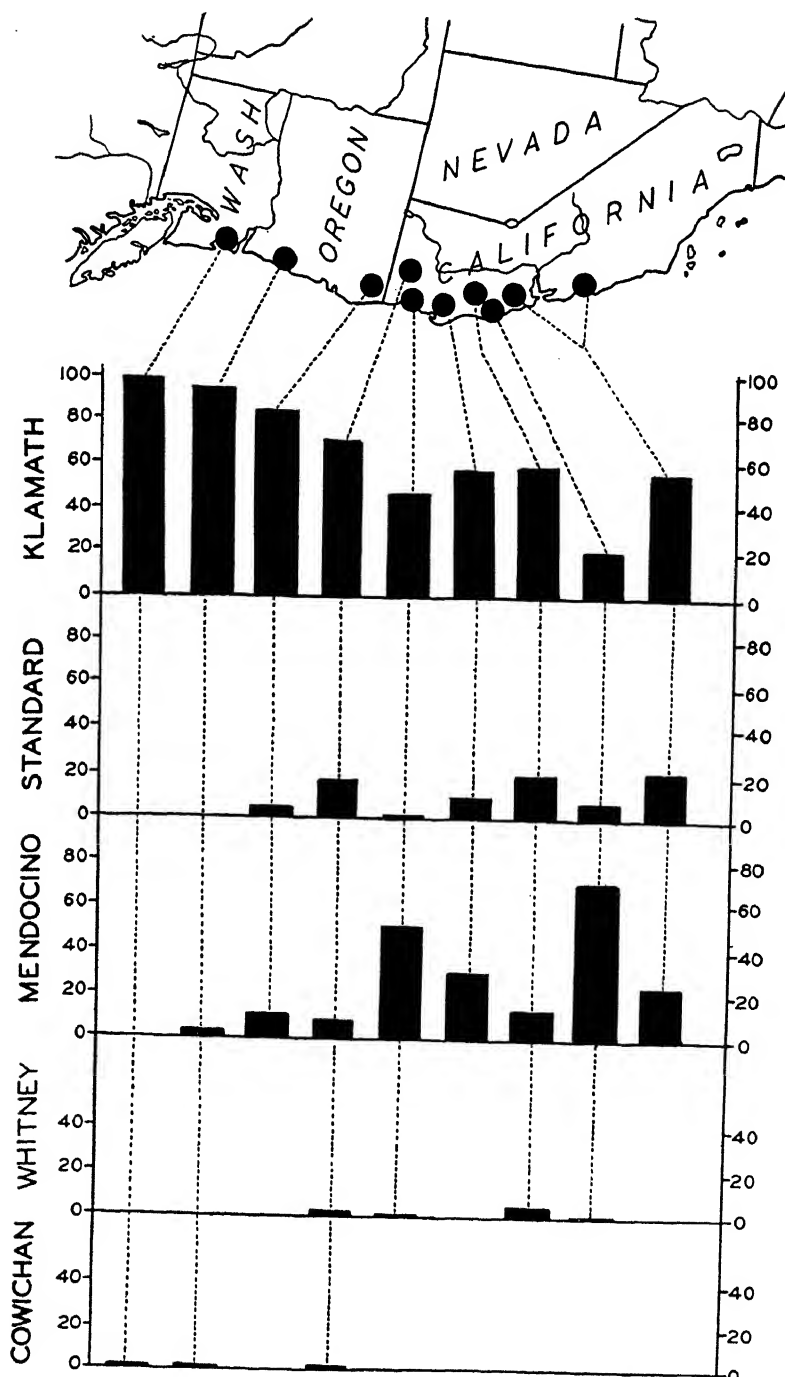
FIG. 14. The Pacific coast populations of *Drosophila persimilis*. For further explanation see figure 10 and text.
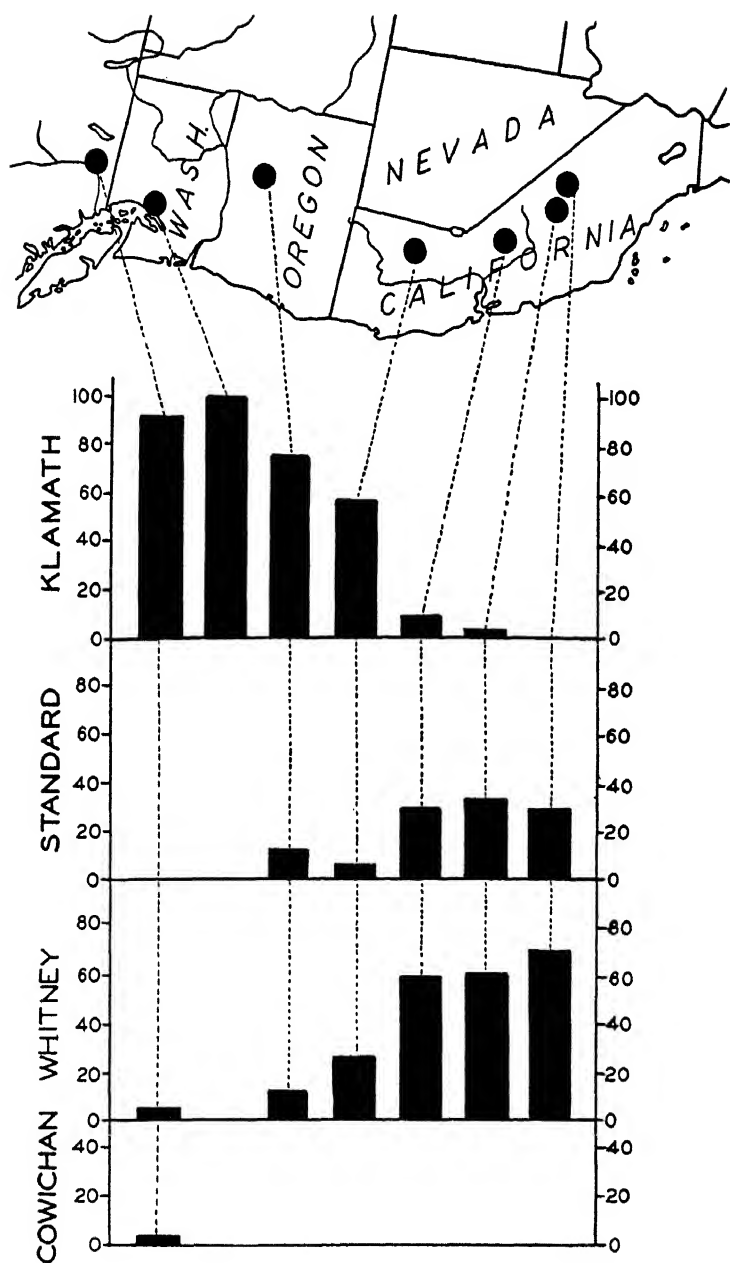
Fig. 15. North-south transect across the distribution area of *Drosophila persimilis*, along the Cascade–Sierra Nevada chain. For further explanation see figure 10 and text.

the southern end of the distribution area. Comparison of the Californian populations inhabiting the Coast Ranges (table 20) with those inhabiting the Sierra Nevada (table 21) discloses a striking difference: the former show high frequencies of Mendocino arrangement and only a few Whitney chromosomes, whereas in the latter populations the relations are reversed. Thus, Mendocino is the characteristic arrangement of the populations of the Coast Ranges, and Whitney is equally characteristic of the Sierra Nevada.

The greater geographic differentiation of *D. persimilis* as compared with *D. pseudoobscura* is probably connected with the differences in the ecological preferences of these two species. As was pointed out in part I, *D. persimilis* is, except along the coast and in the north, an inhabitant of higher elevations in the mountains. The San Joaquin and Sacramento valleys, which separate the Coast Ranges from the Sierra, are in all probability a greater obstacle to migration of *D. persimilis* than of *D. pseudoobscura*. In the north, where the country intervening between the Cascade Range and the Coast Ranges is habitable for *D. persimilis,* populations are considerably more uniform than they are in the south.

Geographic Variation in the Y Chromosome

The variability of the Y chromosome in *Drosophila pseudoobscura* and *D. persimilis* has been described by Dobzhansky (1935, 1937*b*, 1939*a*); only a summary of the results need be given here. Five types of Y chromosome are known to occur in *D. pseudoobscura,* and three types in *D. persimilis,* one of them being common to the two species. The different types are distinguishable at metaphase-plate stage by their lengths and the positions of the spindle attachments; types II, VI, and VII are approximately equal-armed V's, types I and III are unequal-armed V's, and types IV and V are J-shaped chromosomes. The nature of the differences between these types is a matter of conjecture: deficiencies, duplications, and inversions of chromosome segments may be involved. Since the Y chromosome is composed of heterochromatic material, it cannot be identified with ease in the salivary-gland cells; this makes accumulation of statistical data very laborious. Furthermore, since the recognition of the types of Y chromosome is based entirely on their appearance at metaphase, there is no assurance that the chromosomes which are visibly alike are also genetically identical. It is quite possible that the same type has arisen repeatedly and in different places, from different sources and by different means. With these reservations, the geographic distribution of the types of Y chromosome may, however, be used for characterization of the geographic races of the species under consideration.

The west coast (the Pacific Border and Cascade-Sierra provinces of Fenneman) are inhabited by populations of *D. pseudoobscura* which are, as far as known, uniform in having Y chromosomes of type IV. East of the Cascade-Sierra mountains type V definitely predominates, but admixture of type IV is observed in Arizona, New Mexico, and southwestern Colorado (Basin and Range, Colorado Plateau provinces). A rare type, VI, is also found in that

territory. The Rocky Mountains of Colorado (Southern Rocky Mountains province) are populated by types V and VII; the populations of Texas are insufficiently known. Populations of Mexico contain mixtures of types IV and I, the latter having been found once also in southern Arizona (Santa Rita Mountains). Guatemalan populations are, as far as known, pure for type VII. The apparently discontinuous distribution of this type (Guatemala to Rocky Mountains of Colorado) is startling, but the reservation made above must be kept in mind in evaluating this fact.

In *D. persimilis,* Y chromosomes of type I are most frequent, except around Puget Sound (British Columbia and Washington), where a strong admixture of type II is observed, and in the Sierra Nevada and the southern Coast Ranges of California, where type III appears to be prevalent.

There is no rigid correlation between the types of Y chromosome and the gene arrangements in the third chromosome. Nevertheless, a careful comparison of the distributions of these two classes of variants discloses what appears to be a significant parallelism (Dobzhansky and Sturtevant, 1938). The first of the four major subdivisions of the distribution area of *D. pseudoobscura* established on the basis of the variation in gene arrangement (see p. 132), the Pacific Coast division, is characterized by type IV of Y chromosome. The second, the Basin and Range–Colorado Plateau subdivision, has types V, IV, and VI. The third, Colorado to Texas, has, at least in the Colorado part, types V and VII. The fourth, Mexico, shows types I and IV. Only the difference between Mexico and Guatemala in the types of Y chromosome has no parallel in the differentiation of the gene arrangements. In *D. persimilis,* the ·northern populations containing Klamath and Cowichan gene arrangements have mixtures of types I and II of Y chromosome; the southern populations have much Standard gene arrangement and type III of Y chromosome. In the intermediate zone, Klamath and Mendocino gene arrangements in the third and type I in the Y chromosome predominate.

Conclusions

Are the species *Drosophila pseudoobscura* and *D. persimilis* subdivided into races? How many races are there within each of these species? What is the nature of these races? Three fundamental facts emerge from the data. First, both species display individual variability in chromosome structure: individuals which inhabit a given territory, no matter how small, may differ in the gene arrangement in/ the third, X, and second chromosomes, or in the shape of the Y chromosome. Second, both species show group variability: populations inhabiting different territories may differ either quantitatively, in the relative frequencies of chromosomal variants, or qualitatively, if all the members of one population have chromosome structures lacking in another population. Third, the group variability is compounded of the elements of individual variability: any *kind* of difference observed between two populations may occur also between individuals of the same population or between sibs.

The units of individual variability are genes which are represented by two or more alleles (genes represented by a single allele in all the individuals which compose a species are obviously irrelevant so far as intraspecific variability is concerned), and chromosomes which occur in two or more structural types differing in the gene arrangement or in the presence or absence of blocks of genes. The genotype of an individual is a combination of gene and chromosome variants present in the species. Owing to the properties of the mechanism of sexual reproduction, the gene and chromosome combination of an individual need not recur in its entire progeny or even in any of its immediate offspring. If a large number of diverse gene and chromosome variants occur in a population, an individual's genotype may be unique and nonrecurrent. To define a race as a group of individuals with identical genetic constitution is meaningless as regards sexually reproducing organisms. According to such a definition, ultimately every individual would belong to a race of its own. A race is not an individual and not a single genotype, it is a group of individuals, a population, in which many different genotypes occur. It would be equally fallacious to define a race as a group of individuals having a given gene allele or a given chromosomal structure in common. Since in most species there are many variable genes and chromosome structures, and since different genes and chromosome structures are capable of forming a variety of combinations, an individual or a population might belong to one "race" so far as the gene A is concerned, to a different "race" with respect to the gene B, to a still different "race" with respect to C, etc. To be sure, the ideal of genetic analysis is to be able to describe each individual in terms of gene and chromosome variants which it contains. But the race concept is a tool for description not of individuals, but of subdivisions of species. We propose to define races as populations characterized by differing frequencies of the variable genes and chromosome structures. Ideally, all variable genes and chromosome structures would have to be taken into account to describe a given race. At the present level of knowledge this ideal is unattainable. It can be approached by considering as many variational elements as are accessible. The description of races may become more and more exact as knowledge grows.

In accordance with the above definition, the species *D. pseudoobscura* and *D. persimilis* are subdivided into races. Significant differences have indeed been found between many populations which inhabit parts of the distribution areas of these species. Such differences have been established with respect to all the variational elements which have so far been examined. The delimitation and enumeration of the races, however, is quite another matter.

Statistically significant differences may occur between populations of localities only a dozen miles apart, and, in fact, between populations of stations only a fraction of a mile apart. These populations are, then, racially distinct. The composition of a given population may change in the course of time; inhabitants of a territory become racially altered within a few generations. Therefore, races are so numerous that they are practically uncountable, and they are not fixed but constantly changing. Although these facts are very important and

must never be lost sight of in considering the nature of racial variability, the practical application of the race concept must be somehow restricted if this concept is to remain useful. Could one designate as races only such populations as differ qualitatively, in the presence and absence of a group of variational elements? Let us consider what such a restriction would lead to. Populations of *D. pseudoobscura* which inhabit Guatemala have, invariably so far as is known, type VII of the Y chromosome, and Santa Cruz, Cuernavaca, or Estes Park arrangement in the third chromosome. On the other hand, populations of northern Arizona and southern Utah have type V or VI of Y chromosome, and usually Arrowhead, rarely Standard, Chiricahua, or Pikes Peak arrangement in the third chromosome. These populations are, then, qualitatively distinct. Given a mixed sample of Guatemalan and Arizonan individuals, we can unfailingly determine the origin of every specimen. If the species were confined to Guatemala and Arizona, or if we were acquainted only with Guatemalan and Arizonan populations, the situation would be simple enough. But populations of other regions raise difficulties. For example, populations of the Rocky Mountains of Colorado have type V, VI, or VII of Y chromosome, and Arrowhead, Pikes Peak, or Estes Park arrangement in the third chromosome. Are we, then, to distinguish three races? There are numerous other populations intermediate between the three groups just mentioned. Are we, perhaps, to consider that individuals having type VII of Y chromosome belong to the same race regardless of whether they come from Guatemala or from Colorado? This is not reasonable, because such individuals frequently differ in the gene arrangement in the third chromosome and, doubtless, in many other characters. To make the race concept useful we must look for other criteria.

As we examine populations of many localities, it sometimes happens that the frequencies of gene and chromosome structures change gradually in a given geographic direction, so that the differences between the populations are proportional to the distances between the localities which they inhabit. Uniform geographic gradients of this kind may connect populations which are profoundly, qualitatively or quantitatively, different in genetic constitution. The end members of the chain of populations are racially distinct, 'but so are all the intermediate links. A systematist may or may not find it desirable to break the chain of populations into two or more sections and to designate them by racial or subspecific names. If he does so, the divisions are quite arbitrary. His decision will be guided by considerations of expedience and by nothing else: the difficulties caused by the presence of populations intermediate between the arbitrary racial "types" may or may not outweigh the convenience of having simple reference names applicable to some of the populations. On the other hand, the gene frequency gradients may be steep in some regions and relatively level in others. The differences between the populations are not proportional to the distances separating them; the species is broken up into more or less discrete arrays of populations. These arrays can be delimited, counted, and named. This is not because the genetic differences between discrete popu-

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lation arrays are necessarily greater than between the end members of a continuous population chain, but solely because the discontinuities eliminate the arbitrariness of drawing the dividing lines between groups of populations. It is convenient to refer to discrete arrays of populations as races.

In nature, geographic gradients are seldom quite uniform or quite discontinuous. Intermediate situations occur more frequently than the extremes. Within a single species, two races may be easily separable while another two races show only a slight discontinuity. Furthermore, there may be discontinuities of different orders. A species may be split up into two parts showing a considerable break between them, but within one or both of these parts there may exist several minor discontinuities. One investigator may choose to distinguish two major races, and another may describe several minor ones. Which course is adopted is a matter of expedience, judgment, and the conventions which prevail among students at a given time. For example, in the species D. pseudoobscura there is a rather conspicuous break between the populations of the Pacific coast of the United States and those of the Intermontane Plateau; between those of the Intermontane Plateau and those of the Rocky Mountains and Texas; and between those of the United States and those of Mexico and Guatemala. Four races might, then, be distinguished. But within at least two of these four races there are rather clear secondary discontinuities, and there is little doubt but that such secondary discontinuities will be found within the other two races when more material is available. We may choose to distinguish four, or seven, or more races. Or, since the minor as well as the major races are connected by gradients, we may refuse to delimit any races at all.

Whichever course is adopted, the realities of the situation are not altered in the least. It remains true that the species D. pseudoobscura and D. persimilis are geographically differentiated: populations of different territories differ in the relative frequencies of chromosomal types. This is what is meant by racial differentiation. Given an individual from any part of the distribution area, we can predict the probability that it will have a given gene arrangement in the third chromosome, that it will or will not carry the "sex ratio," that it will have a certain type of Y chromosome. Given a population sample from a known locality, we can predict the probable frequencies of the chromosomal variants in it. We can also infer the country of origin of a population sample if we know its genetic constitution. Racial studies are successful to the extent to which such predictions are fulfilled. But it should never be forgotten that a specimen of D. pseudoobscura from California which carries the Santa Cruz gene arrangement in the third chromosome is in that respect more similar to specimens from Mexico which have the Santa Cruz gene arrangement than it is to other California specimens, perhaps even to its sibs, if the latter carry Standard, Arrowhead, or other arrangements. The intraracial variability is commensurable with the interracial variability. The genotype of an individual is only to some extent determined by the population from which it sprang. To what extent, depends on the degree of the racial differentiation present in the species.

SUMMARY

1. The gene arrangements in the right limb of the X, in the second, and in the third chromosomes, and the shape of the Y chromosome are variable within the species *Drosophila pseudoobscura* and *D. persimilis*. All the variations in gene arrangement can be accounted for by the occurrence of inversions of blocks of genes in the phylogeny.

2. Fifteen gene arrangements in the third chromosome occur in natural populations of *D. pseudoobscura,* and seven in *D. persimilis.* One of these arrangements is common to the two species. The gene arrangements in other chromosomes are relatively more constant. The reason for the greater variability of the third chromosome is unknown.

3. Intraspecific variations in the gene arrangement in the right limb of the X chromosome are associated with the "sex ratio" phenomenon, that is, with the production of almost unisexual progenies.

4. All the chromosomes which carry a given gene arrangement have arisen probably from a single ancestor. The same arrangement seldom, if ever, arises repeatedly in the phylogeny.

5. Inversions which arise in natural populations are mostly single. Multiple inversions are formed probably exclusively by succession of independent inversion steps.

6. The descent relationships of the gene arrangements have been established. The ancestral arrangements in the third chromosome have been determined with a fair degree of probability. The phylogeny of the gene arrangements is, therefore, known.

7. Some of the gene arrangements in the third chromosome are relatively widespread, others are endemic to smaller territories; none occur throughout the species area.

8. Only rarely is the population of a locality homogeneous with respect to a gene arrangement in the third chromosome; two or more, up to seven, arrangements may occur side by side. Homozygotes and heterozygotes for gene arrangements are formed, and their relative frequencies are in accord with Hardy's equilibrium. It follows that panmixia prevails in the populations, and that the viabilities of the homo- and heterozygotes are very nearly alike.

9. Statistically significant changes in the relative frequencies of gene arrangements can be observed in some populations within a few months. There are reasons to believe that such temporal changes follow the seasonal climatic cycle.

10. Populations of localities a few miles apart may differ in the relative frequencies of gene arrangements to an extent greater than the amplitude of the temporal fluctuations.

11. Populations which inhabit remote territories are, as a rule, more different than those of adjacent or near-by territories. The frequencies of a given gene arrangement may form geographic gradients or "clines," that is, they may increase or decrease more or less regularly in a given direction.

12. The frequencies of the "sex ratio" in *D. pseudoobscura* form ascending gradients from north to south. The same is probably true for *D. persimilis*.

13. Geographic gradients for the third-chromosome gene arrangements are much more complex than those for the "sex ratio" (figs. 10–15).

14. With respect to the gene arrangements in the third chromosome, four major subdivisions may be distinguished within the species *D. pseudoobscura:* (*a*) the Pacific coast of the United States and the Sierra Nevada–Cascade mountain chains, (*b*) the Intermontane Plateau, (*c*) the Rocky Mountains and Texas, and (*d*) Mexico and Guatemala. Secondary subdivisions are indicated within the four major ones.

15. Three major subdivisions are found in *D. persimilis:* (*a*) Washington and Oregon, (*b*) the Coast Ranges of California, and (*c*) the Sierra Nevada.

16. Geographic variation in the Y chromosome is in general correlated with that in the third chromosome.

17. Races are defined as populations of a species which differ in the incidence of one or more variable genes or chromosome structures. In accordance with this definition, there is a multitude of racial subdivisions of different orders within *D. pseudoobscura* and *D. persimilis*.

18. Which order of racial subdivision should be described and named in taxonomic practice is a matter of convenience and of conventions prevailing at a given time. The delimitation of races is arbitrary if the variations of the gene and chromosome frequencies within a species follow uniform geographic gradients. If discontinuities are present, the delimitation of races is not arbitrary, but it remains a matter of taste, expediency, and convention whether the investigator chooses to name only the major or both the major and the minor subdivisions of a species.

19. In any case, the intraracial variability is commensurable with the interracial, and the genotype of an individual is only to some extent determined by the "race" from which it sprang.

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PLATES

Camera lucida drawings of chromosome configurations in *Drosophila pseudoobscura* and *Drosophila persimilis*. In most cases only the critical parts of the chromosomes are represented; the parts which failed to show a clear disk pattern in the preparations drawn are shown by outlines only. The numerals refer to sections of the standard chromosome maps. The scale in plates 3 and 4, common to all four plates, represents microns.
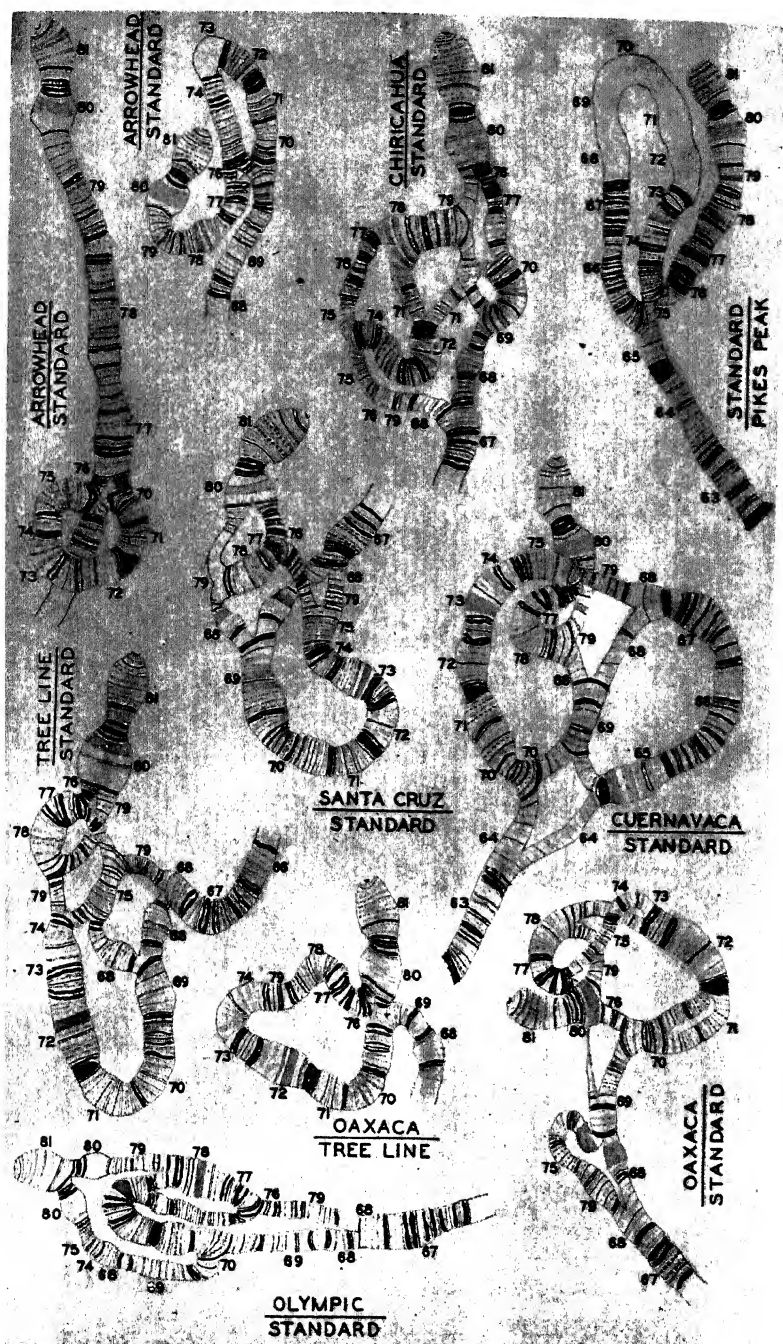
THIRD CHROMOSOMES OF *Drosophila pseudoobscura*
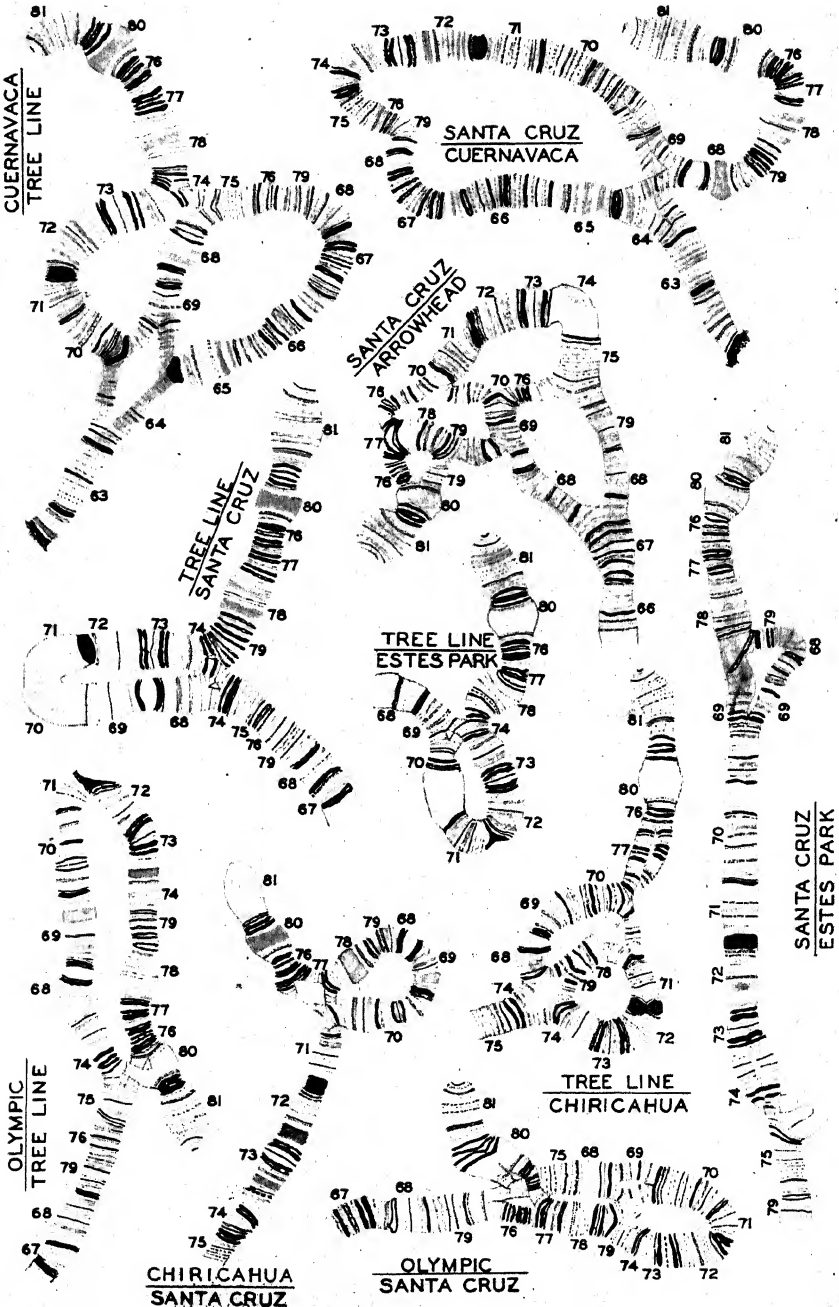
THIRD CHROMOSOMES OF *Drosophila pseudoobscura*

THIRD CHROMOSOMES OF *Drosophila pseudoobscura*

PLATE 4
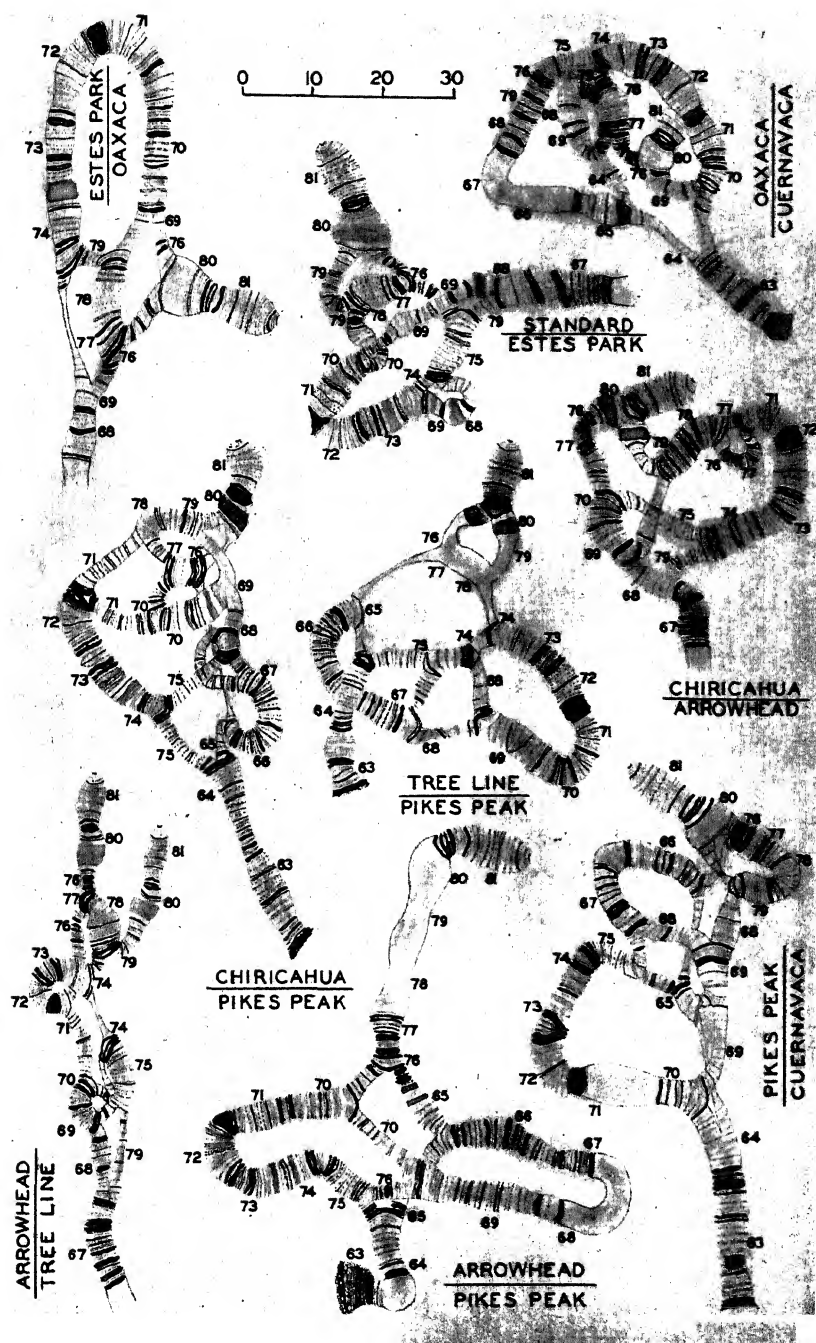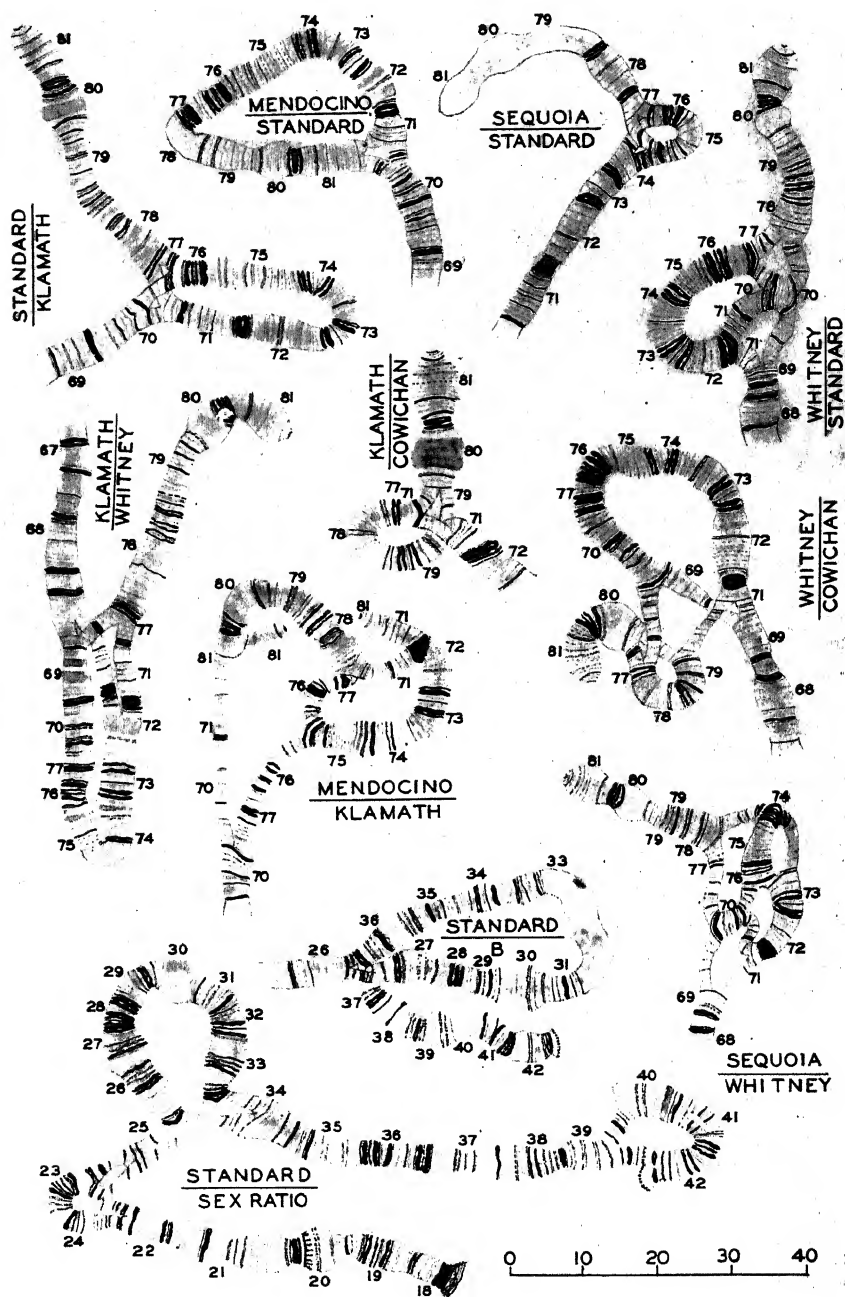
THIRD CHROMOSOMES OF *Drosophila persimilis*, AND RIGHT LIMBS OF X CHROMOSOMES OF
Drosophila pseudoobscura AND *Drosophila persimilis*

III

The Historical Background

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CONTENTS

III

The Historical Background

THE PROBLEM [1]

The fact has been amply demonstrated in parts I and II that the geographical distribution of the gene arrangements of *Drosophila pseudoobscura* and *D. persimilis* presents an orderly pattern both with respect to the presence and absence of certain gene arrangements and with respect to their relative frequencies. Future exploration will doubtless augment and may modify the pattern which they form, particularly in the northern Rocky Mountains and in the Sierra Madre Occidental, both of which regions are very inadequately sampled. But we are confident that its main outline is known, particularly with respect to frequency dominance, and that sufficient data are now at hand to discuss the causes which may have produced it.

Unlike most physical attributes which are geographically expressed, the gene arrangements have this important quality, unique for such a discussion, that their phylogeny has been determined with a high degree of probability, one can almost say with certainty. Hence, any hypothesis advanced to explain this pattern must take into account the distribution of each arrangement relative to its phylogeny. The facts must also be borne in mind that, so far as is known, the gene arrangements are attributes which are equal in selective value, and that no genetic barrier exists which might tend to segregate them (part II).

It has been shown in part II (fig. 5 and accompanying text) that the fifteen known gene arrangements of *D. pseudoobscura* and the seven of *D. persimilis* do not exist as simple linear phylogenetic sequences. Of this number, any one of three, but of three only, Standard, Hypothetical, and Santa Cruz, may be taken as ancestral. But given one as the initial arrangement, then all others become fixed in their relative positions. Furthermore, there are reasons for believing that Hypothetical, the existence of which has thus far only been inferred (see p. 63), may represent the initial arrangement. However this may be, Santa Cruz and Standard are the primary arrangements of three phylogenetic sequences or phylads, which we shall designate as the Santa Cruz phylad, found only in *D. pseudoobscura;* the Standard phylad of *D. pseudoobscura;* and the Standard phylad of *D. persimilis.*

Four regularities of primary importance can be discerned in the distribution of these phylads. (1) The gene arrangements are found in greatest number in two areas, the Pacific slope in California and the highlands of central Mexico and Guatemala (fig. 1).[2] (2) The areas in which the gene arrange-

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[2] See also the detailed data of distribution in tables, figures, and text of part II.

ments of wider distribution are dominant in frequency correspond generally to the principal physiographic, climatic, and biotic subdivisions of the specific area (fig. 2). (3) The distribution of the Standard and Santa Cruz phylads is significantly different (fig. 1). The former is dominant in the United States, is largely absent from Mexico, particularly central Mexico, and is apparently entirely absent from Guatemala. It is centered in California. The latter is dominant in central Mexico and is centered there. (4) The Santa Cruz phylad, except the arrangement Chiricahua, is broken into three disjunct areas: (a) the Pacific slope in California; (b) the region extending from the Rocky Mountains to central Mexico, separated from the first named by the deserts of the Basin and Range province; (c) the highlands of Guatemala, separated from the second by the tropical region of the Isthmus of Tehuantepec (fig. 1). Chiricahua is exceptional and has been found throughout most of the specific area except in Guatemala, where its presence cannot be excluded. The fact that it is centered in the intermediate region—for it appears to be dominant in the Sierra Madre Occidental, and is the most abundant arrangement of its phylad in the Basin and Range province—is noteworthy.

Our problem is to account for these regularities.

Discussion

The concentration of various gene arrangements in various parts of the whole specific area suggests that they may have been segregated there by climatic factors. This may be true in part. Yet the occurrence to some degree in the most diverse climates of homozygotes of the widespread arrangements contradicts such a view. Evidence has already been presented in part II (p. 101) which suggests that the gene arrangements are themselves equal in viability. Furthermore, the evidence presented in part I with respect to the habitat of D. pseudoobscura and its seasonal cycles and diurnal periodicity suggests that it is able to tolerate a wide range of climates as diverse as those of Puget Sound or Lake Atitlan and Yuma, Arizona, through adaptation to a relatively narrow partial climate, and that it is essentially continuous throughout the area. Hence, although climate may have operated in some way to produce the geographic differentiation of the arrangements and their frequency dominance, it is difficult to understand how it alone could have produced the wide separation of some of the arrangements.

Before any explanation can be undertaken, the question must first be answered whether these arrangements are in fact segregated, as they appear to be. A positive answer can almost certainly be returned with respect to the populations found in central Mexico and Guatemala, because in this instance the flies do not in all likelihood occur in the intervening territory. In both Guatemala and Mexico, the species is confined to a relatively narrow altitudinal belt in the temperate forest of the highlands, and occurs infrequently or not at all at lower elevations, even in the lower zones of that forest. In view of our general knowledge of the distribution of plants and animals, we are accordingly bound
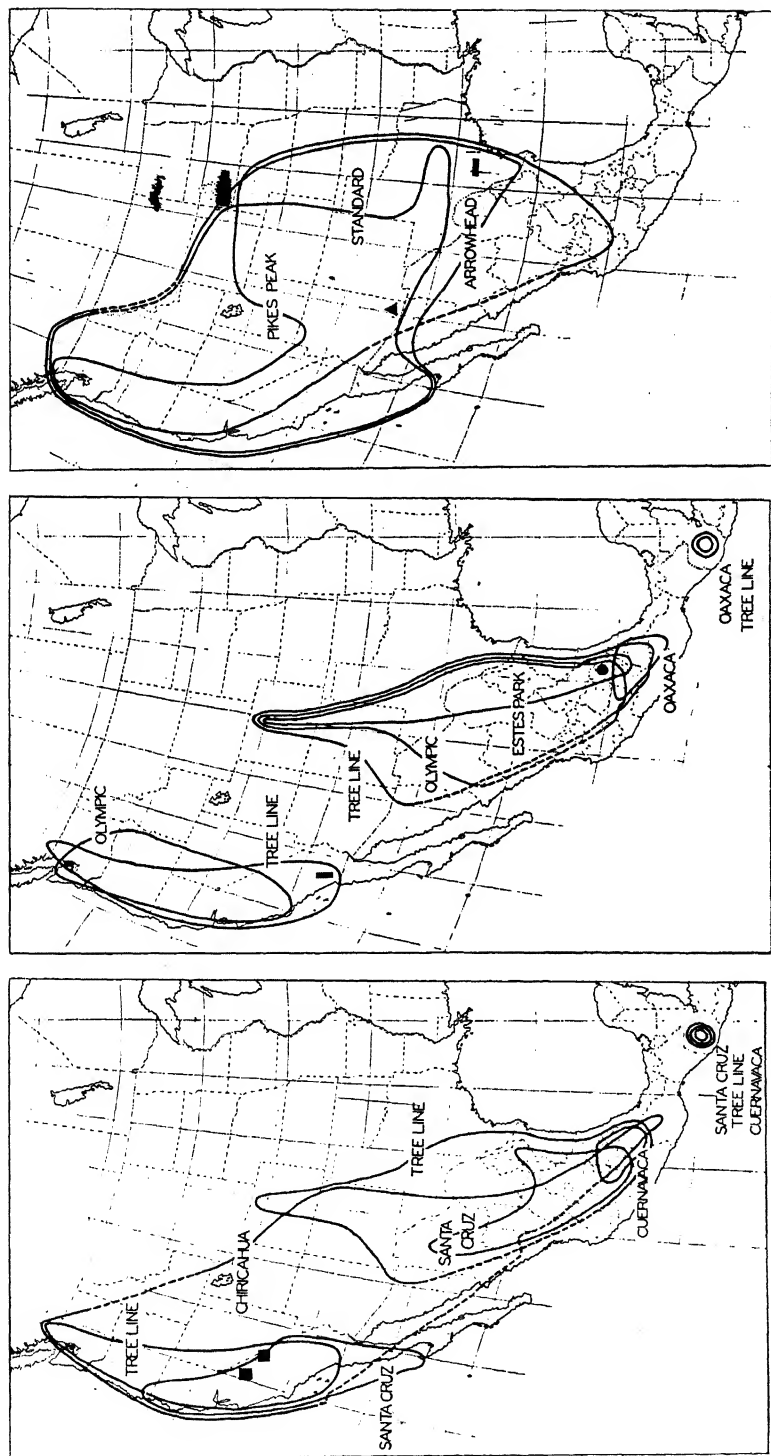
Fig. 1. *Drosophila pseudoobscura.* (Left) limits of the primary and secondary arrangements of the Santa Cruz phylad; (center) limits of Tree Line and its derivatives; (right) limits of the Standard phylad. The symbols indicate the location of arrangements found in only one or two localities: square, Mammoth; circle, Hidalgo; vertical bar, San Jacinto; triangle, Cochise; horizontal bar, Texas. See also part II, figures 6, 7, 8.

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to doubt its existence in the tropical forests of the low-lying Isthmus of Tehuantepec.

With respect to the arrangements Santa Cruz and Olympic, the answer is less certain but still positive. We know that the *species* inhabits the territory between the two parts of their range. But the Colorado Desert, which lies between, constitutes a partial barrier of considerable magnitude, for we know from repeated observation that the flies are present there only in low concentration and that their ability to breed in abundance is restricted to occasional favorable periods. It is possible that these arrangements may be found to be continuous by way of Baja California, Sinaloa, and Nayarit, as was suggested in part II. Yet this connection seems improbable for the same reasons we have already advanced. As one proceeds southward along the peninsula of Baja California, particularly below the Viscaino Desert, which is similar in vegetation to the Colorado, and still farther southward along the coast of Sinaloa, the vegetation becomes more and more tropical. It is accordingly doubtful whether the species occurs there. If any connection exists, it seems much more probable that it lies by way of the Sierra Madre Occidental at increasingly higher elevations. We have fairly abundant collections from the Colorado Desert, and from the outlying ranges of the Sierra Madre in southern Arizona (Huachuca and Chiricahua mountains). Neither Santa Cruz nor Olympic has been found in them. There is good reason to suppose, therefore, that Santa Cruz and Olympic in the areas in question are separated by several hundred miles of intervening territory. The same argument applies to Tree Line, although in this case the distance is less and the populations may eventually be shown to be continuous.

Even though Santa Cruz and Olympic should eventually be found throughout the Sierra Madre, their areas would still be separated by the breadth of the Colorado Desert. That this desert is in fact a barrier to the spread of these arrangements is strongly suggested by the proportions of Santa Cruz which have been found on Mount San Jacinto, which borders the desert, but is still relatively humid and coastal in climate. In approximately 11,000 chromosomes studied, Santa Cruz has been found only 38 times; Olympic is unknown there. Even though we assume a phase during the pluvial periods of the Pleistocene sufficiently humid for piñon woodland to spread more widely and to form a connecting reticulum, a barrier still would apparently have existed, for no Santa Cruz is known from the Basin and Range province, where piñon woodland is widespread at present (and even more humid forest at higher elevations) and in which relatively abundant collections of flies have been made, for instance in northern Arizona.

Three explanations occur to us which might account for this wide separation: (*a*) the occasional independent origin of the same arrangement, (*b*) the transport of flies from one area to another, introducing an arrangement new to the area, and (*c*) the operation of historical factors.

Evidence has been advanced in part II which indicates with a considerable degree of certainty that the probability of repeated origin of the same inversion is very small and that, at most, such repetition would be rare. We can

now only suggest in addition that if such is the case, it seems highly improbable indeed that a sequence of inversions of the first, second, and third order should have arisen independently in two or perhaps three separated areas: Santa Cruz → Tree Line → Olympic on the Pacific slope and in central Mexico (and possibly also in Guatemala); Santa Cruz → Tree Line → Oaxaca in central Mexico and in Guatemala. Hence, we must look to one or both of the other two possible explanations: the transport of individuals from one region to another, and the operation of historical factors. The only agent of transport which seems adequate or likely in this case is wind (for a discussion of wind as an agent of transport see Darlington, 1938).

Existing conditions of air turbulence, particularly in the arid regions of the southwestern United States, provide an excellent vehicle for lifting individuals to great altitudes whence they might be carried far and wide, and we know that *Drosophila* has been trapped from an airplane at elevations of at least 1000 feet (Glick, 1939). Whether the insects would survive such an aerial journey is unknown; they are very fragile and easily killed. That they avoid direct sunlight suggests the possibility that exposure to its full intensity might be detrimental or even fatal. Yet occasional individuals might successfully overcome whatever hazards exist. Even so, once arrived at a new habitat, their limited range of flight might prevent their finding a suitable feeding and breeding place. Furthermore, the evidence for the sedentary nature of the populations which has been presented in parts I and II suggests that any such successful journeys are infrequent. But only an occasional one would need to be accomplished to produce widespread dissemination of any given arrangement in the course of geological time.

We can judge to some extent whether wind has been a factor in distribution of the insects over wide areas in comparatively recent times by the degree to which the pattern of distribution is in accord with the pattern to be expected from the direction of the prevailing winds. Along the Pacific coast of the United States, the prevailing winds, both winter and summer, are predominantly onshore. This is also the case in winter along the Pacific coast of Mexico. But in summer the prevailing winds of Mexico and Guatemala are from the Caribbean and follow a generalized track which sweeps in a wide arc northwestward along the Cordillera and ultimately toward the lower Mississippi Valley. Their effect infrequently reaches as far as southern California. It is generally assumed by meteorologists that these phenomena have not varied greatly since the Pleistocene, or even earlier, inasmuch as the conditions which produce them have probably not changed materially in recent geological time. We might accordingly expect to find the distribution of the gene arrangements in the United States to be prevailingly from west to east and the distribution in Mexico to be prevailingly from southeast to northwest.

In a general way this is what we do find (fig. 1).[1] The Standard phylad in the United States ranges in a general easterly direction. Standard, particularly,

[1] See also part II, figures 12–15.

shows a fairly regular gradient from California to the Rocky Mountains. In Mexico the distributions bear from south to north. Yet on closer consideration discrepancies appear which are difficult to explain; particularly, the absence of certain arrangements where they might be expected, and the north-south alignment of the Santa Cruz phylad on the Pacific slope, athwart the Standard gradient.

Standard, it is true, can readily be explained as having spread from the Pacific coast eastward by the occasional transport of individuals over a long course of time into territory farther and farther removed from the source. The distribution of Arrowhead, too, might possibly be referred to the same cause; although this arrangement is more abundant in the Great Basin and often the only one found there, nevertheless its gradient from west to east is fairly regular. But Pikes Peak is quite rare on the Pacific slope, is scarcely more abundant in the Great Basin, and occurs in abundance only in Texas. It has also been found at three localities in Mexico, far to the south, where Standard is unknown and probably does not occur. We might assume that at one time Pikes Peak was abundant in the west and has since disappeared there, but there is no evidence to support such an assumption. Or we might assume that it arose in Texas; but if so, how can we account for its progress to the Pacific slope without invoking some other agency than the winds?

Of the Santa Cruz phylad, Chiricahua, Santa Cruz, and Tree Line are all found on the Pacific coast, their frequencies being in the order named. The distribution gradient of Chiricahua in the United States somewhat resembles that of Standard, decreasing from west to east, although, as was pointed out above, it is probably the dominant arrangement in the Sierra Madre Occidental. If Chiricahua and Standard could be carried eastward, why not Santa Cruz, which is an arrangement perhaps as ancient as Standard and certainly older than its derivative Chiricahua? If it is a question of relative frequency at the place of origin, why then should Tree Line reappear in the Rocky Mountains? Why, also, should it be absent from the Great Basin, although Chiricahua is relatively abundant there? There seems to be no satisfactory answer to these questions. Furthermore, how might one account for the presence in central Mexico and Guatemala of Santa Cruz, carried there presumably against the prevailing winds? And if one assumes that at some time or other the winds may have carried the insects southward from California, why, again, should Chiricahua be found in the intervening area, but not Santa Cruz, its parent arrangement? If Chiricahua and Santa Cruz, Tree Line and Olympic were carried southward, why not also Standard? for Standard is presumably as old, or nearly as old, as Santa Cruz, and Olympic is a tertiary arrangement. It will be remembered that homozygotes of these arrangements have been found in diverse climates and that even though we assume a slight difference in selection potential, which is contrary to the evidence, they might still persist as heterozygotes.

We might assume that Santa Cruz originated in Mexico and was the initial arrangement. Blown northward, it might have established itself on the Pacific

coast.in California, where Standard came into existence and ultimately Arrowhead and Pikes Peak. But its derivatives Chiricahua, Tree Line, and Olympic must also have been carried there, or else have originated there independently, a contingency which we have already shown to be highly improbable. If Santa Cruz was transported northward, why not Cuernavaca, Estes Park, and Oaxaca also, all widespread and fairly abundant in central Mexico, and, in part, in Guatemala? They might not have been in existence, of course, when this event took place, if it occurred only once; yet Cuernavaca is a secondary derivative, whereas Olympic is tertiary, derived through Tree Line. Even if we grant these possibilities, how still can we account for the distribution of Pikes Peak? Furthermore, how might we account for the spread northward to British Columbia of Chiricahua, Tree Line, and Olympic across the path of the prevailing winds, if not against them? And if of these, why not of Santa Cruz?

We cannot exclude the possibility that wind has caused the present distribution pattern in recent time. But the only tenable conclusion seems to be that, if such is the case, the factors are so variable in effect that a consistent explanation is impossible at present.

But let us assume that the disjunctions observed are only apparent and not real, and that future exploration will show that all arrangements can be found in very low concentration in all parts of the area. We might then call on the wind to account for these occasional individuals, yet still have found no explanation of the pattern as a whole, particularly with respect to the dominance of the various arrangements in correlation with the principal climatic and biotic regions.

In the foregoing discussion we have considered principally the transport of flies over long distances. Let us consider now an example of possible transport over shorter distances. We have already alluded to the sporadic and limited occurrence of *Drosophila persimilis* in the Coso and Panamint ranges of California (p. 91), to the east of the Sierra Nevada, where this species is abundant at higher elevations. These are arid ranges which are marginal in habitat to the prevalent conditions under which the species exists. The distance from the Sierra to the Panamint Range is approximately 50 miles. The intervening area is desert in which it is improbable that the species exists unless in low concentration. The arrangements found are the predominant ones of the Sierra. That occasional winds may carry this species from the Sierra Nevada to the Panamints cannot be denied, and, indeed, seems probable. Nevertheless, even here an alternative view is possible, because of the apparent correlation of the distribution of *Drosophila* in this region with that of the associated biota.

Three principal biogeographic areas exist in the western United States, each of which corresponds to one of the principal physiographic areas (classification of Fenneman, 1928): that of the Pacific slope (Pacific Mountain System), that of the Great Basin (Intermontane Plateaus), and that of the Rocky Mountains (Rocky Mountain System). Many species and genera are confined to, or are characteristic of, one or another. Nevertheless, many species range widely from the coastal areas eastward into the mountains of the Great Basin, of which the

Panamints are a part, or to the Rocky Mountains. At the same time, species characteristic of the Great Basin ranges or of the Rocky Mountains, or species of genera which are characteristic of these regions, may extend westward into the Sierra Nevada. The biota of the Panamint and Coso ranges is predominantly that of the Great Basin, and most of its elements extend eastward. But among the species which range eastward from the Pacific coast many have outlying stations in the Panamint Range. A few, such as *Juniperus occidentalis*, a characteristic tree of high elevations in the Sierra Nevada and found also in the North Coast Ranges, reach their eastern limits there, just as *D. persimilis* does. Hence the view is certainly tenable that, although the colonies of *D. persimilis* in the Panamint and Coso ranges may have been initiated by the occasional transport of individuals by wind, they may also be populations relictual from a time when the biota of these mountains was more closely connected with that of the Sierra Nevada. In other words, we might consider these populations of the species to be not casually but historically connected, and their separation the product of an historical process. By this we mean a complex of concomitant environmental factors in operation over a prolonged period.

We can test this view by applying it to the distribution of the gene arrangements. Do they show any correlation with the trends in distribution of the biota as a whole? For the United States, and for the Standard phylads both of *D. persimilis* and of *D. pseudoobscura,* the answer is fairly simple and positive. They do. For the Santa Cruz phylad the answer is positive but less simple.

Let us first consider the Standard phylad of *D. persimilis*. As was shown in part II (p. 132), three principal centers can be discerned. Klamath is predominant in the Pacific Northwest, and in some samples from that region was the only arrangement found. It extends to the southern Sierra, where it is infrequent. Mendocino is the predominant arrangement of the North Coast Ranges, is frequent in the Sierra Nevada, and reaches into Oregon. Whitney is predominant in the southern Sierra, is infrequent along the coast of California, and ranges into Washington. In addition, Standard and Sequoia are largely confined to California, and Cowichan to Washington and Oregon. Wawona is known from only one locality. The forest biota of California, Oregon, and Washington is closely related and forms one of the major biological communities of the western United States. But it is not uniform over this area. The biotas of Oregon and Washington are more like each other than either is like that of California. Nevertheless, the division is by no means a sharp one; many species characteristic of Oregon and Washington range southward along the Sierra Nevada or along the Coast Ranges, and conversely, many species characteristic of California may range to British Columbia. Within California, the biota of the North Coast Ranges, although similar and closely related to that of the Sierra Nevada, differs from it in many respects. In other words, the distribution of the gene arrangements of this phylad parallels that of the biota as a whole.

A similar parallel exists between the distribution of the gene arrangements of the Standard phylad of *D. pseudoobscura* and the biota of the region over

which it is found. We have already mentioned the three principal biogeographic areas of that region. Standard is characteristic of the biota of the Pacific slope, and, like some well defined species of that region, as well as many generic phylads, extends in decreasing frequency to the Rocky Mountains. Arrowhead is characteristic of the biota of the Great Basin and extends into both the Pacific and the Rocky Mountain provinces, just as do many of its associates. Likewise, Pikes Peak is characteristic of the southern Rocky Mountains and western Texas, and, like some elements of that region, reaches sporadically to the Pacific slope.

The distribution of the Santa Cruz phylad in the United States is similar, but is complicated by two features: the discontinuous distribution of certain arrangements, and the relation of all to similar populations in Mexico. In the United States, Santa Cruz, Tree Line, and Olympic are found on the Pacific slope. Tree Line and Estes Park are found in the southern Rocky Mountains and the southern sections of the Basin and Range province and the Edwards Plateau; thence they range southward to central Mexico. But in the intervening area in the Basin and Range province, Chiricahua appears to be the principal if not the sole member of this phylad and extends southward along the Sierra Madre to central Mexico. In this phylad also the distribution of the arrangements parallels, although less precisely, both the three biogeographic communities mentioned above and also the distribution of the members of the Standard phylad. In the United States these arrangements are always of relatively small frequency, hence conclusions are less certain. But it seems probable that, within this phylad, Santa Cruz (like Standard) is the most common in maritime situations in California, Chiricahua (like Arrowhead) is more abundant inland and seemingly more characteristic of the Great Basin, and Tree Line (like Pikes Peak) is the most common in Texas and the southern Rocky Mountains.

In Mexico and Guatemala the data are far from abundant. Nevertheless it appears fairly certain that Santa Cruz, Cuernavaca, and Oaxaca are confined to the temperate forests of central Mexico and Guatemala. Santa Cruz is seemingly the predominant arrangement in west central Mexico and Guatemala, Cuernavaca in east central Mexico, and, as was pointed out above, Chiricahua is thought to be dominant in the Sierra Madre Occidental. Although not dominant, Estes Park seems to be most abundant in eastern Mexico or in Colorado. Here also, the distribution of the gene arrangements conforms to the principal biogeographic areas. As is suggested by the correspondence of arrangements in central Mexico and Guatemala, the relationship between the temperate biotas of these two regions is especially close, many species and phylads being represented in both. The flora of northeastern Mexico, which ranges to east central Mexico, is often extended into western Texas and sometimes into the southern Rocky Mountains. The flora of northern Mexico is closely related to that of the Great Basin.

Another more general relationship can also be discerned between the central Mexican region and the Pacific slope. In the Pacific Mountain System a rela-

tively high rainfall reaches its maximum from November to March, during which the temperature reaches its minimum (fig. 2). In the Volcanic and Sierra del Sur provinces of central Mexico (classification of Thayer, 1916) and in Guatemala, a relatively high rainfall reaches its maximum from May to October, during which season the temperature also reaches its maximum. These extremes, each characterized by a difference in the seasonal incidence of rainfall with respect to temperature, are connected by a gradient from northwest to southeast which is modified in the intervening territory by the low rainfall which characterizes the interior Intermontane Plateaus and the north Mexican plateau.

The nature of this gradient is shown graphically in figure 2. The bar diagrams are constructed to show the precipitation-evaporation ratios by months, computed according to Thornthwaite's method (1931, 1933), for selected stations throughout our area in the United States. Each station is situated near, and records conditions of rainfall and temperature similar to those of, stations at which flies have been collected. The data on which the diagrams are based were obtained in part from published Weather Bureau records and in part from the U. S. Forest Service, through the courtesy of E. I. Kotok. This method was employed to permit comparison of the climates which distinguish different parts of our area, because it combines rainfall and temperature in a way which appears to reflect the effect of climate on the distribution of flora and fauna. Because of the lack of comparable records, it has proved impracticable to compute such data for Mexico and Guatemala. The incidence of rainfall relative to temperature, however, is essentially the same throughout our area in Mexico, and it seems probable that all of a series of such bar diagrams arranged from north to south would resemble the diagram shown for Fort Davis, with a proportionate increase during the summer months as one progresses southward. The southernmost would probably form an approximate reciprocal of some of the Pacific coast stations, such as Eureka or Seattle. In lieu of diagrams showing the precipitation-evaporation ratios, bar diagrams are shown for rainfall only (Page, 1930), for the "southern plateau rainfall province," which would include most of our collection stations in central Mexico and would correspond roughly to the Volcanic division; for the "southern west coast rainfall province," which would include those in Oaxaca, and would correspond in general to the Sierra del Sur division; and for the "northern plateau rainfall province," which would correspond in part to the north Mexican plateau.

The specific area can therefore be described as one of great diversity of environment, but one in which a relatively simple gradient can be traced. The geographic extremes, the Pacific coast of California, Oregon, and Washington on the one hand and the highlands of central Mexico and Guatemala on the other, are relatively mild, humid, and equable. They are essentially maritime climates. The intervening territory becomes progressively drier, with greater extremes of climate, and progressively more continental in type, until the arid deserts of the southwestern United States and adjacent Mexico are reached.
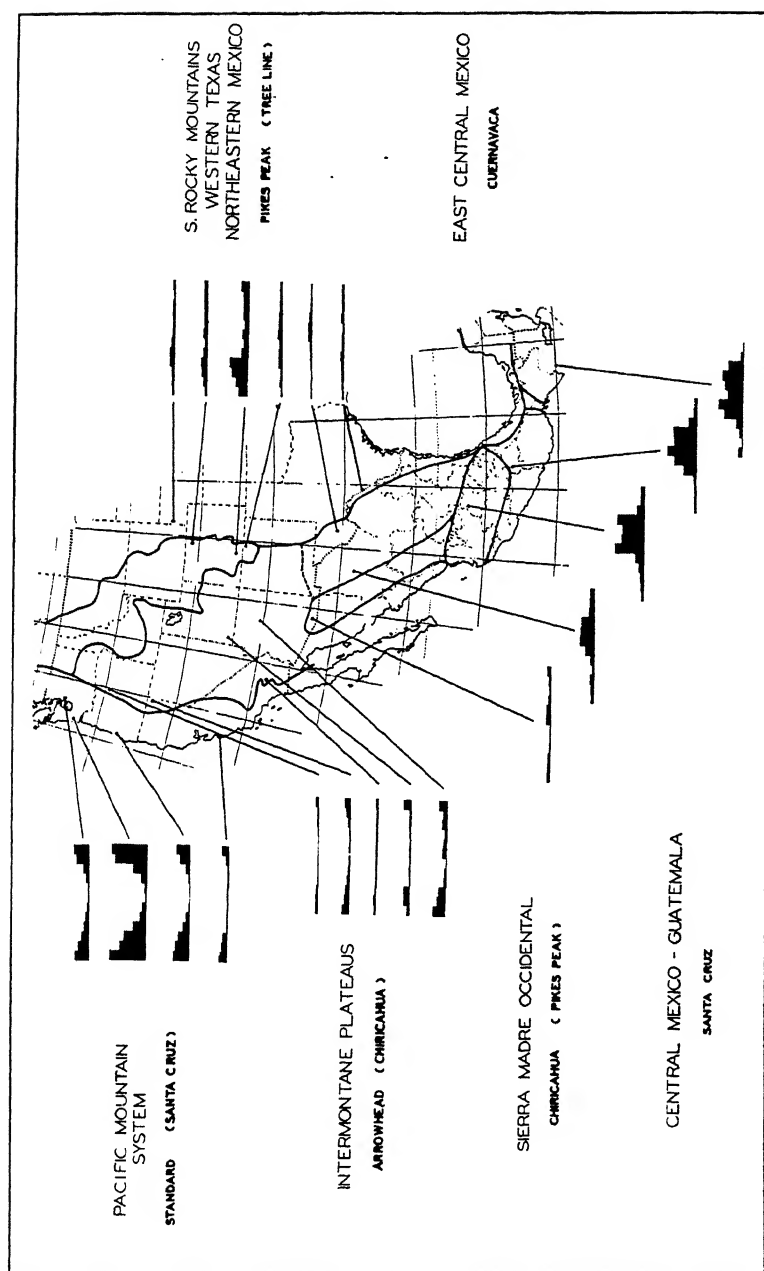
FIG. 2. *Drosophila pseudoobscura*. Distribution of the dominant arrangements with respect to frequency. Explanation in the text. The arrangements shown in parentheses are the dominant ones within the phylad which in that area is secondary in frequency.

It is noteworthy that these two geographic extremes, both of which are characterized by mild and equable climates, should prove to be two parallel centers of concentration of the Santa Cruz phylad. Along the Pacific slope, centering in California, Santa Cruz, Tree Line, Olympic, Chiricahua, Mammoth, and San Jacinto are found. In central Mexico, Santa Cruz, Tree Line, Olympic, Chiricahua, Cuernavaca, Estes Park, Oaxaca, and Hidalgo are found. In the intervening areas only Chiricahua, Tree Line, and Estes Park are found, all of which also occur in one or both of the principal areas, but none of which is restricted to either. These facts of distribution and phylogeny may be only a striking coincidence, but unless the gene arrangements in each arose independently, as seems highly improbable, it is reasonable and justifiable to infer that these two populations were at one time continuous and that the territory which now intervenes, or at least that part of it which the population then occupied, also had a mild and equable climate. Within this inference lies the implication that some gene arrangements later became restricted and that others expanded. This implication might suggest that the present distribution is a function of climatic change, which we have shown is probably not the case, so far as the gene arrangements themselves are concerned, for they have been found equally viable wherever they have been tested. But the possibility still exists that the various arrangements may have arisen in populations which were already differentiating with respect to different genes or gene frequencies which might restrict the population to certain habitats, or permit it to expand into others.

The literature of systematic biology is replete with examples of disjunct distribution of species and of groups of closely related species or subspecies, from which it is inferred that the now disjunct populations are historically connected. For many of these no alternative casual explanation is acceptable or reasonable. Several with which the writer is familiar at first hand will be discussed as examples. *Salvia sonomensis* is a distinctive Californian species which is widespread but highly localized. Its principal area lies in central and northern California. In southern California it is known only from four neighboring localities in San Diego County, which are separated from the nearest known locality in the north by approximately 350 miles. In itself this distribution is not necessarily remarkable, and might justifiably be attributed to chance seeding, although the intervening territory seems to offer favorable habitats which are not occupied. But this species is paralleled by a number of other species of diverse habit which have a similar disjunct distribution between San Diego County and the north. In view of our knowledge of past movements and shifts of vegetation in this region, the more plausible explanation is that the two populations are historically connected, and that the San Diego population is a relict. Another striking and similar example of now disjunct distribution has been brought to the writer's attention by Harlan Lewis, and is mentioned because the cytology of the forms in question has been investigated. *Trichostema oblongum* is found in northern California and ranges along the Sierra Nevada from Fresno County northward to Washington and northern Idaho. It is

diploid. Paired with it is a second and tetraploid species as yet undescribed, which is found in southern California in the San Bernardino and San Jacinto mountains and in San Diego County. One widely disjunct colony has been found, however, near Gull Lake in Mono County, on the eastern slope of the Sierra Nevada, 350 miles distant from the nearest colony in the San Bernardino Mountains and separated from it by the Mojave Desert. This distribution is not exceptional, for many species of the San Bernardino and San Jacinto mountains also range northward to the southern Sierras and the Argus, Panamint, and Providence mountains. The most reasonable explanation of these facts is that the now widely separated populations were at one time a single population.

Many other examples of disjunct distribution of the members of a species pair (or of subspecies) might be advanced. Several have been described by Lewis and Epling (1940), and Stebbins (1942) has recently discussed the striking example of the species of *Dirca*. The casual transport of seed can scarcely be appealed to in such instances, unless we assume that specific differentiation has occurred subsequent to transport. Examples can readily be found in many families, moreover, in which one widely disjunct member of a species group is endemic to a restricted area which is characterized by a high endemism in general. In such instances a casual explanation seems out of the question. For example, we might cite the Cuban province of Pinar del Río and the Isle of Pines. This restricted area is characterized by numerous narrow endemics. Among them are two species of *Hyptis, H. pedalipes* and *H. eriocauloides,* and a species of the related group *Eriope,* as yet undescribed. The first named is a member of the species group *Cyanocephalus,* of which the remaining species, twenty in number, are found in Brazil and adjacent Paraguay. The second is a member of the distinctive group *Plagiotis,* of which another species is found in São Paulo and Paraná and a third in British Guiana and eastern Colombia. The genus *Eriope,* consisting of approximately twenty species, is found in Brazil and adjacent Paraguay, save for the one species mentioned above. Again, the only reasonable explanation is that these populations are historically connected and have been subjected to the impact of the same factors for a prolonged time.

In transferring this course of reasoning to the distribution of the gene arrangements of *Drosophila pseudoobscura* and *D. persimilis,* we are fortunate in that we can appeal not only to facts of the present distribution of the biota of the western United States, but also to facts known regarding its past distribution, from which we can infer past climates and topography and the major trends of the movement of the biota. Such inferences may frequently be misleading, or, as is sometimes shown by later evidence, quite fallacious, as pointed out by Sears (1935, p. 37): "To reconstruct the vegetation of the past involves, as does any historical research, numerous sources of error and confusion. Yet reconstruction is necessary if we are to understand the changing environment of the past or to interpret modern vegetation," and we conclude with him that in the absence of direct evidence "there is no escape from considerable, legiti-

mate, inference based upon geology as well as upon living plants and communities believed to be relicts of past conditions."

Two periods suggest themselves during which the Pacific slope of California and central Mexico may have been joined by a more equable, mild, and humid climate than now exists in the territory between them, and when opportunity was at hand for an exchange of populations; namely, the pluvial periods of the Pleistocene, and the Tertiary.

We shall first attempt to infer the distribution of the western biota during the Pleistocene and the probable effects of glaciation on its movements. We shall undertake particularly to ascertain whether the Basin and Range province and the desert of southeastern California and Arizona may have been sufficiently humid, mild, and equable in climate at that period to resemble the present areas in which Santa Cruz, for example, is found, and whether we can rightly infer that the populations which carry that and other disjunct arrangements were then continuous. If so, we can then conclude that the major facts of present distribution of the gene arrangements can be explained as Pleistocene or post-Pleistocene phenomena. If not, we must look to an earlier period in the world's history.

Summary

Because their phylogeny has been established with a high degree of certainty, we are interested here in the geographic distribution of the gene arrangements relative to one another. In the spatial pattern which they form we can discern four regularities for which we seek an explanation: (1) The gene arrangements are found in greatest number in two widely separated areas which are nevertheless more similar climatically than the intervening regions; (2) certain gene arrangements are dominant in frequency in areas which correspond in a significant degree to the principal biotic subdivisions of the specific area; (3) the distribution of the Standard and Santa Cruz phylads is significantly different; (4) the Santa Cruz phylad is broken into three widely disjunct areas, a disjunction which is apparently real, with the exception of one gene arrangement, which is centered in the intervening region. The predominance of certain arrangements is not the result of climatic assortment of the arrangements themselves, for they have been shown to be equally viable under the conditions in which they have been tested and also are known to occur as structural homozygotes in widely different climates. The disjunction of some arrangements is not, in all probability, the result of independent origin of the same inversion, nor does it seem probable that it is the result of casual transport by wind. The view that the whole pattern is the product of an historical process seems more plausible. This view is based on the correlation which exists between the distribution of the gene arrangements and the distribution pattern of the biota of the specific area. Furthermore, the two centers of concentration of the gene arrangements of the Santa Cruz phylad, which exist under the mild and equable conditions of a maritime climate, suggest

also an historical correlation with climate. Although the gene arrangements are not themselves amenable to climatic segregation, the possibility remains that they may have arisen in populations differentiating in gene frequencies in such a way that the population might become restricted to a given environment or might expand beyond it. If these phenomena have been historically produced, then a period must be sought when climatic conditions were such that the relictual populations at the two centers of concentration (in California and in central Mexico) might have had a connection. This period may have been during the pluvial periods of the Pleistocene, or may have been earlier.

PLEISTOCENE BIOTA AND CLIMATE

Inferences which may suggest the nature and distribution of the Pleistocene biota can be drawn from four sources, namely, (1) the geological and meteorological facts of glaciation themselves, together with the theories which have been advanced to account for them; (2) the paleontological data of the glacial period; (3) the nature of the vegetation which followed the retreating ice, as indicated by the analysis of pollen from Pleistocene or post-Pleistocene bogs which were marginal to the ice; and (4) the present distribution of vegetation with respect to the glaciated territory. We shall examine each in the order listed.

Two views exist concerning the climatic conditions which led to glaciation. The first of these, which stems largely from the studies of Alpine glaciation, suggests a general lowering of summer temperatures, rather than an increase in precipitation. The second, which appears to stem largely from the studies of European vegetation, suggests rather an increase in precipitation (for a review of these arguments and bibliography see Antevs, 1928; also Antevs, 1922, 1925b, 1929, 1932, and Hultén, 1937). These views are seemingly contradictory, yet they are of importance in evaluating the effect on the displacement of the biota, inasmuch as a widespread lowering of summer temperatures would imply a corresponding widespread dislocation of the biota, whereas an increase in precipitation, accompanied by a similar or even higher mean temperature, as suggested by Simpson (see below), might imply a more regional effect; controlled in part by the degree of shift in the position of the summer storm track, with reference to the topography of the land masses.

That living glaciers advance and recede in response to cyclic changes in weather is well known. Such fluctuations have been studied by Reeds (1929), and the belief has grown that they are ultimately induced by changes in solar radiation. Arctowski, for example, the latest investigator in this field, has reached the conclusion (1941) that "solar variation is a weather element of wide and complex influence." Whether it is also a factor in climatic change cannot be directly established. Simpson (1938) has suggested that this is indeed the case and that the glacial period was initiated by an increase in temperature which resulted from increased solar radiation. He points out (ibid., fig. 5) that two complete oscillations in solar radiation can account for the three interglacial periods, of which two would be warmer and wet, and the median one

colder and dry, and concludes that we are now approaching a minimum of solar radiation. He resolves the apparent contradiction which the evidence of Alpine glaciation had introduced, by the suggestion that the glacial climate of the Alps and the consequent lowering of summer temperatures were influenced by local conditions.

He points out that the ice sheet was centered in northeastern North America and in northwestern Eurasia, and not at the pole, because of the existence of the polar sea, the shores of which are known to have been in part unglaciated, and believes that the flow of ice throughout the year from the polar sea, together with the absence of the gulf drift from the western coasts of Europe and the displacement of the Icelandic depression, were sufficient to account for the lowering of summer temperatures in the region concerned. Inasmuch as there was no corresponding flow of ice into the Pacific, glaciation on the Pacific coast of North America would have been relatively scant and local.

From the meteorological evidence and hypotheses discussed in these papers there is, therefore, reason to believe that the mean temperature of the earth's surface during the glacial epochs may have been somewhat greater than at present and that the rainfall increased, a belief which finds general acceptance among meteorologists; and that any lowering of summer temperatures may have been only local, induced by the immediate effect of the ice, by the movements of air, and by increase in elevation. Hence, the glacial climates are believed to have been either approximately as at present or wetter and somewhat warmer.

These conclusions relate to the Pleistocene climate in general. But we are particularly interested in the climate of the southwestern United States during that period. One might assume that with an increase in precipitation the Southwest would have become relatively humid. This does not appear to have been the case; on the contrary, because of the conformation of land masses "an arid belt must have existed then, as now, between the region of predominantly ascending air in the middle latitudes and the similar region at the equator" (Sverdrup, oral communication). The position of this belt in the Southwest and its approximate rainfall can be surmised from the evidence of the Pleistocene lakes and the Pleistocene floras.

Meinzer (1922) has shown very plainly the relation of latitude to the size and abundance of these lakes. Most of them were crowded in the northern part of the Great Basin in the region of the two giant lakes Lahontan and Bonneville. "Farther south the lakes were smaller and less abundant, and some large basins contained no lakes of sufficient size and permanence to leave distinct shore features. In southwestern Arizona lakes were absent, because there were no closed basins that could hold lakes, but in southeastern California and trans-Pecos Texas closed basins occurred, and the absence or scarcity of lakes in these parts of the province was apparently due to aridity. . . . The rapid transition from central Nevada, with its abundant Pleistocene lakes, to the relatively desiccated region of southern Nevada and southeastern California is largely due to rapid decrease in altitude with great increase in temperature

and evaporation. Lake Estancia, in central New Mexico, whose strand is 6200 feet above sea level, was one of the highest of the Pleistocene lakes, and consequently, though it lies far south, it occupied 22½ per cent of its basin. Lakes Bonneville and Lahontan evidently owed their great size to the productivity of the lofty Wasatch Mountains and Sierra Nevada, respectively." Meinzer concludes that the "relatively humid parts of the province at the present time seem to be comparable to the most, arid parts of the Pleistocene epoch. The region of southwestern New Mexico and southeastern Arizona in the Pleistocene is apparently comparable to southern Oregon at present, for the Pleistocene lakes near the Mexican border do not seem to amount to much more than do the present lakes of Oregon. The south end of Nevada in the Pleistocene can perhaps be compared to northeastern Nevada at present, with its few small lakes, the difference in latitude here being less than in the first case because there is a great difference in altitude. Parts of southeastern California and trans-Pecos Texas in the Pleistocene can perhaps be compared to parts of Nevada at present, where the climate is just too arid for perennial lakes."

It is reasonable to conclude that although the mountains which surrounded the Great Basin may have received more rainfall than at present, this rainfall diminished southward rather sharply. The mean change in precipitation necessary to produce the greatly augmented Pleistocene lakes is uncertain. Even with the present low rainfall the remnants fluctuate greatly from year to year (Antevs, 1925a, 1938), and, although this results in part from the fact that most of them lie shallow on the flat bottoms of the ancient lakes and evaporation is correspondingly great, it seems probable that a relatively small mean increase in rainfall on the surrounding mountains would account for their size during the pluvial periods. We can conclude, therefore, that the southern part of the Basin and Range province was nearly as arid during the Pleistocene as at present, particularly if the mean temperature was higher. This conclusion is supported by the paleontological evidence which we shall now examine.

On the Pacific coast the principal data which relate to Pleistocene vegetation have been obtained by Chaney and his associates (Chaney and Mason, 1930, 1933; Potbury, 1932; Mason, 1934; and Frost, 1927). Of the floras described, four have been found in southern California: on Santa Cruz Island, which lies off the coast south of Santa Barbara; at Carpinteria, a few miles east of Santa Barbara on the mainland; at Rancho La Brea, now within the city of Los Angeles; and at McKittrick, in western Kern County, north of Santa Barbara in the arid southern part of the Great Valley and separated from the three coastal sites by the South Coast Ranges and the Tehachapi Mountains.

In summarizing the Willow Creek flora of Santa Cruz Island, Chaney and Mason (1930) conclude that it probably represents a community which had much in common with the present coastal forest at Fort Bragg, California, approximately 450 miles farther north, although the more northern elements of the present Fort Bragg flora are not represented. This comparison implies an extensive shift in vegetation; yet there seems to be no reason for postulating a climate very different from the present one at Monterey, scarcely 200

miles north, as suggested by A. H. Miller (1937). One of the fossil species, *Pinus remorata,* is still resident on Santa Cruz Island, and all the fossil species can now be found in the vicinity of Monterey, except *Pseudotsuga taxifolia,* which occurs sporadically at higher elevations in the Santa Lucia Mountains somewhat to the south and east of Monterey and at lower elevations some-what farther north, near Santa Cruz. (H. L. Mason states that the Vegetation Type Map of California shows a single individual on a ridge above Monterey [oral communication].)

The Carpinteria flora investigated by the same authors (1933) lies across the channel which now separates Santa Cruz Island from the mainland. It is similar in composition to the Willow Creek flora, but contains a more xeric element, indicated by *Juniperus californica* and *Pinus Sabiniana* (or *Coulteri*) as well as the abundance of *Arctostaphylos* fruitlets. This element, however, bears evidence of transport, presumably from a more arid interior. *Pseudotsuga taxifolia* is represented only by driftwood (as also *Sequoia sempervirens*). The main element of this flora closely resembles the present closed-cone pine forest of the Monterey peninsula, and because of its similarity to the Willow Creek flora it is dated as approximately contemporaneous. The presence of *Ceanothus thyrsiflorus* and *Pyrus Hoffmanni* (allied to *Pyrus rivularis*) in the flora certainly suggests a somewhat moister environment than that of the present, although Mason states that *C. thyrsiflorus* still occurs at Point Conception (oral communication).

The Rancho La Brea flora from the coastal plain of Los Angeles, described by Frost (1927), is similar but meager. It was said by him to represent *Pinus tuberculata, Cupressus macrocarpa, Juniperus californica* var. *breaensis, Quercus agrifolia, Celtis Douglasii* (*C. mississippiensis* var. *reticulata*), and *Sambucus caerulea* (*S. glauca*). Mason states, however, that the pine is in fact *P. muricata* and that the cypress can be equally well referred to *C. goveniana* (oral com-munication). If this is the case, as seems likely, then the Rancho La Brea flora is represented in the Carpinteria flora by all the species except *Celtis Douglasii.* Except for that species, the climatic difference indicated by the dif-ferences in determination would not be significant. *Cupressus goveniana* and *C. macrocarpa* both occur on the Monterey peninsula at present, and *Pinus tuberculata* ranges from Del Norte County to San Bernardino County, east of the Rancho La Brea deposit. The presence of the *Celtis,* which is known at present only along the margin of the desert, suggests a somewhat more arid flora, however, especially since it is associated with *Juniperus.*

H. L. Mason has recently described the McKittrick flora in a paper now in press, the manuscript of which he has considerately made available for study. He finds that the identifiable species, six in number, are living in the California flora today and present a harmonious ecological assemblage, not unlike an assemblage in the modern flora of the northeastern part of Santa Barbara County, south of McKittrick, and consistent with the assemblages of birds and mammals with which it is associated (Miller and De May, 1942; Dice, 1925; Compton, 1937; A. H. Miller, 1937; L. Miller, 1942; De May, 1941).

The La Brea deposits were referred by Hay (1927) to the first interglacial, the Aftonian. This conclusion has been carefully reviewed by Schultz (1938), who, on the basis of faunal evidence, sees no reason for an earlier date than the last interglacial, the Sangamon, or the period of the Wisconsin sheet itself. He considers the Carpinteria, McKittrick, and La Brea deposits to be approximately contemporaneous.

Whether the Santa Cruz flora is contemporaneous with the more arid Carpinteria, McKittrick, and La Brea floras and differs from them chiefly because of local influences, as may indeed have been the case in view of the Pleistocene elevations, or whether it represents a different phase of the Pleistocene, when precipitation was greater than today, is as yet impossible to determine. Chaney and Mason (1930) suggest that there is good reason to believe that the Santa Cruz locality of the Pleistocene was peninsular and subject to maritime influences. Perhaps because of such influences, analogues of *Pinus remorata* and *Cupressus goveniana* (*P. muricata* and *C. Forbesii* or *C. guadalupensis*) are still able to grow as far south as northern Baja California, Cedros Island, and Guadalupe Island, the latter almost as far south of Santa Cruz Island as Fort Bragg is north. In view of the persistence of fragments of this Monterey flora as far south as Cedros and Guadalupe islands, the climatic changes since the Pleistocene may have been relatively small. George O. Hale (unpublished) has concluded that the distribution of the groves of *Pinus muricata* on Cedros Island is correlated with the position of high fog streamers, and it would appear that the pine is still able to persist there surrounded by the *Larrea* formation of the Colorado Desert because of this relatively slight cloud effect.

The more southerly distribution along the coast and on Santa Cruz Island, during the Pleistocene, of such species as *Pseudotsuga taxifolia* and *Ceanothus thyrsiflorus* suggests a greater rainfall there than at present. This suggestion is corroborated by the present occurrence on the Channel Islands of relicts such as *Vaccinium ovatum*, known now on the mainland only farther north,[1] and associated there with the humid coastal forest. On the other hand, the occurrence of *Juniperus californica* in the Carpinteria, McKittrick, and La Brea floras, and of *Celtis Douglasii* in the Carpinteria, suggests a somewhat more arid climate on the coastal plain and in the interior of southern California, or perhaps simply a warmer climate, possibly comparable with that of San Diego County today, as implied by A. H. Miller (1937), or, as Mason suggests (*in* Compton, 1937), with that of the southern slopes of the Tehachapi Mountains. The species of the La Brea flora all occur today in the mountains of San Diego County and *Pinus muricata* occurs in northern Baja California at Pine Canyon near San Antonio Mesa, associated with the Diegan flora (Epling and Robison, 1940; Epling and Lewis, 1942). It is also of interest to note that *Juniperus californica* occurs above the coastal llano a stone's throw from the ocean near the mouth of the Río San Ysidro. This locality is not far removed from the stand of *Pinus muricata* and *Cupressus Forbesii* in Pine Canyon.

[1] Since the above was written Mason has informed the writer that *Vaccinium ovatum* has been found on Roderick Mountain in San Diego County.

The consensus of opinion of the students of the Pleistocene of California seems to suggest, therefore, that at that time the coastal areas may have been somewhat more moist, or mild, perhaps because of the topography then existing, and that the interior had an arid aspect perhaps no less than that of today. This opinion has been well summarized by A. H. Miller (1937, p. 252) as follows: "If we let our fancy run, and for the moment pass over the problems of time intervals within the Pleistocene, we can imagine California to have been as sharply subdivided zonally in the immediate geological past as it is at present, with the same general distribution of zones. On the coast and in the north there was a greater expansion downward or southward of Transition areas, particularly a more extensive and continuous coastal pine forest. In the south, coastwise and in the interior, there was no restriction of the arid areas, but some climatic differences which favored a heavier, though arid forestation, at least locally on the coastal plains. Southern California resembled northern Lower California in abrupt contrasts, yet had certain northern components not now found in Lower California. Northern California was of more boreal aspect. The net result was a remarkable series of contrasts, especially well reflected in the biotas of Carpinteria, McKittrick and Rancho La Brea."

At the northern extreme, in Alaska, much closer to heavy glaciation, Chaney (1936b) has mentioned a Pleistocene or possibly post-Pleistocene deposit in the frozen muck and gravels near Fairbanks, which indicates a vegetation and climate similar to that of today; he finds no evidence of a boundary between the Pleistocene and Recent, with respect either to physical conditions or to biota.

Information on the biota of the Basin and Range province during this period is even more meager. Merriam (1915, see also 1918) has reported on a small mammalian fauna collected near Pyramid Lake, Nevada, which, from the evidence of deposition, suggests that the animals lived and died along the shores of the former Lake Lahontan and were buried in its sediments. If so, they presumably lived during the last interglacial, when precipitation was increased and the ice was melting. Merriam correlates them with the La Brea fauna. If this correlation is correct, then it would appear that the climate of the interior was relatively warm and arid. Hay (1927), however, has confirmed the finding, probably near Salt Lake City, of a skull which he provisionally refers to the musk ox, *Symbos cavifrons.* The age of the animal is indeterminate, but was presumably Pleistocene. This find would suggest a tundra region, either in the Great Basin or in the Wasatch Mountains, which are known to have been glaciated. But such evidence does not necessarily contradict that from Pyramid Lake, 500 miles to the west.

These data from the Basin and Range province are admittedly scant. Yet it must be emphasized that there is as yet no evidence to suggest any other than an arid region, roughly comparable with that of the present.

In the eastern United States Pleistocene floras are few, but they also suggest communities not dissimilar to the present ones. One has been described by Berry (1907) from Alabama in an area which was subsequently submerged.

He likens it to other deposits of similar age in Virginia and in North Carolina. The plants, which were found in peat and in the overlying Pleistocene clay, are all characteristic of the present flora, but with a somewhat different grouping of species. Berry concludes that the climate was probably not very different from that of the present.

Brown (1938) has recently reported on Pleistocene deposits of preserved plants and certain animal remains from Louisiana which he considers to be synchronous with the period of maximum glaciation. The flora is predominantly warm temperate, and consists chiefly of characteristic species of the present-day flora in that region. There is, however, a distinct minor element of more northern species, consisting of conifers and mosses (and certain mollusks), the most remarkable of which is perhaps the white spruce, *Picea glauca*. It is possible that these northern elements penetrated this far south by way of the Appalachians, as Brown suggests.

The regions which we have been discussing, except that at Fairbanks, lay at a considerable distance from the ice sheet, and would have been affected chiefly by local glaciation. The nature of the biota which existed at the front of the ice can be inferred from the nature of the vegetation embedded in bogs which were formed along the front of the ice as it began to recede. This glacial and postglacial climate and vegetation has been reviewed by Sears (1932, 1935; see also Hultén, 1937).

Research on the flora and fauna of Pleistocene central Europe points strongly to the presence of a tundra belt between the Scandinavian ice sheet and the Alps. This tundra, apparently less extensive farther east, was bordered by steppe and forest belts or by park-steppes (see Antevs, 1928, for a review). That a belt of tundra may also have existed in the Middle West is suggested by the remains of musk ox which have been found outside the glaciated area (Hay, 1924). But in North America, as has been pointed out by Sears (1932; see also Berry, 1926), pollen deposits in bogs suggest rather that forest may have bordered the ice front at no great distance, even as it does today in Alaska. (For examples of the inferences which are drawn from the analysis of such bogs, see the investigations of Cooper and Foot, 1932, and Voss, 1933.) We have already referred to Simpson's explanation of the apparently colder climate of unglaciated central Europe, which produced tundra there although it was not generally developed elsewhere along the ice. That a climax forest can exist adjacent to an advancing glacier, be overwhelmed by it on its advance, and quickly reoccupy the denuded area on its recession has been shown by Cooper (1923). On the other hand, the observations of Griggs (1934) and Bowman (1934) on the advance during historic time of the *Picea* forest on Kodiak Island suggest that the tundra along the Alaskan coast is still being invaded. We can only conclude, therefore, that, although the ice sheet may have been bordered by tundra, occurrence of this community may have been sporadic and was seemingly limited; for the most part, apparently, the ice was bordered by forest.

That relatively little displacement of vegetation in the middle-western area accompanied the period of the Wisconsin was long since postulated by Gleason (1922, p. 65; see also Penhallow, 1907) on the ground of present-day distributions. "All these facts of modern distribution may be explained by postulating a glacial climate during the Wisconsin considerably drier than at present and not much different in temperature, so that the vegetation of extra-glacial Illinois assumed a xerophytic aspect. Under this view, we may assume that the Ohio valley in southern Indiana and Illinois was occupied by its present forest flora, possibly not so luxuriantly developed; the Illinoian drift to the north of it by a xerophytic forest of southeastern affinity with a slight admixture, decreasing toward the west, of a prairie element; western Illinois was exclusively prairie, of a type similar to that now prevailing possibly 400 miles farther west. A narrow and interrupted strip of coniferous forest followed the glacial boundary, especially in places where greater topographic relief afforded better shelter. Toward the east, across Indiana and Ohio, the strip became broader and included more species. Toward the north it broadened out again in the driftless area in the shelter of the deep rocky ravines, with the additional protection of the projecting Des Moines lobe of ice extending southward to the west of them. It is doubtful if any conifers or associated species occurred west of this lobe. . . . The presence of an old flora in the Ozarks indicates that this shift did not extend much farther toward the south."

The flora of the Ozarks, referred to by Gleason, has recently been described and its origins have been discussed by Steyermark (1934), who also suggests that the ice sheet had a relatively local effect on the biota to the south of it. This region, unglaciated itself but lying adjacent to the ice, now supports a temperate hardwood forest. There is no evidence that this forest suffered any very marked displacement during the Pleistocene, but on the contrary it appears to be of great antiquity. Steyermark (p. 233) concludes that it consists of two geologically diverse floras: "1) an ancient relic flora common to the southern Appalachians and Ozark region, and dating back in all probability to the uplift that occurred at the close of the Cretaceous, and 2) a younger flora, characteristic of the uplands and barrens of the Ozarks, a flora which probably originated in Tertiary times when this region was re-elevated in late Tertiary."

Summary

From the evidence which has been discussed in the foregoing pages, we can infer with some confidence that, although the structure of the Pleistocene biota was different from that of the present, particularly with respect to the composition of various plant and animal communities, and although some of its elements have since disappeared, the relative distribution of its principal ecological phases resembled that of the present, except within the glaciated regions and along their periphery (but see also Hultén, 1937). The increase in rainfall which apparently characterized certain parts of the period apparently did not greatly affect the Pacific Southwest, and although the presence of the

ice sheet doubtless caused a shift in the storm track, there is reason to believe that even during the pluvial periods the biota of the Pacific coast was separated from that of the Rocky Mountains, as now, by a relatively arid Basin and Range province. There is the possibility of course that in the uplands the pine and oak woodland-savanna may have been more continuous than at present, or even the more mesic forest. If this was the case, in view of our knowledge of relicts it would seem reasonable to expect traces in this inter-vening region of a previous continuous population of Santa Cruz if it had existed in such a Pleistocene woodland, or even more humid forest. It would also seem reasonable to suppose that a Pleistocene connection of the Californian and Mexican populations by way of the Rocky Mountains would have left some trace. None has been found. (Note also the distribution of *D. azteca* and its gene arrangements; see part I and below.) Furthermore, there is evidence to suggest that the Pacific Southwest has been arid since the Pliocene and even earlier. In order to follow the history of the western biota during the Tertiary, its changes and movements, we shall now briefly review the paleobotanical evidence which bears on that subject.

Tertiary Biota and Climate

The belief is generally held by geologists that the continent of North America had reached approximately its present shape by the beginning of the Cenozoic era. The evidence from the fossil record, however, indicates that at that time the relief was not so marked as at present. The Appalachians had been a land area since about the end of the Paleozoic. Parts of the western cordilleras had risen during the Jurassic and Cretaceous, but were evidently in low relief. The principal differences in outline during the Cenozoic were to be found along the Atlantic coast from Long Island to Mexico and along the Pacific coast in western Oregon and southern California. In these areas emergence and submergence occurred at various periods; the most extensive was the transgression of the Mississippi embayment during Eocene time.

The earliest flowering plants make their appearance in the fossil record in the middle part of the Lower Cretaceous of Greenland as components of an otherwise Jurassic flora, and somewhat later in North and South America, in Eurasia, in Africa, and in Australia. (See Seward, 1931, pp. 384, 389–393; for evidence of Mesozoic holarctic dispersion see Fernald, 1931; Chaney and Sanborn, 1933, pp. 28–39; Stebbins, 1941; also Berry, 1919.) They increased in variety and number during the Upper Cretaceous, accompanied still by a dwindling number of older Mesozoic genera, and by the Eocene the recorded floras had become essentially modern. Not only were many of the more generalized families to be found, but several highly specialized families as well, and many familiar genera, some of which were already holarctic in distribution, are recognizable beyond reasonable doubt. The distribution of this vegetation was not uniform, but was zoned according to latitude and, as today, presented a gradient from the tropics northward.

During the Eocene, the southern half of the United States and the west coast as far as Oregon and Washington were occupied by a hardwood forest which verged toward the tropical, particularly in the coastal lowlands. The relationships of this forest in the eastern United States were chiefly with the present Antillean flora and that of eastern South America; on the Pacific coast its relationships were chiefly with the western flora of present-day Central America and northern South America, but it also embraced elements in common with the Pacific floras of the Old World tropics and had a secondary relationship with the Antilles and the southeastern United States. Throughout Holarctica at higher latitudes ranged a temperate forest, the Arcto-Tertiary, dominated by gymnosperms, notably *Sequoia* and *Taxodium,* but embracing many temperate hardwoods. In the farthest north it passed into an impoverished cool-temperate forest (Berry, 1916*a, e,* 1922, 1925, 1930, 1937; Chaney, 1936*a,* 1938*b,* 1940*a, b;* Chaney and Sanborn, 1933; Sanborn, 1935; Potbury, 1935; La Motte, 1935; MacGinitie, 1937*a, b,* 1941; Clements, 1916, pp. 356, 362; Bradley, 1929; Kryshtofovich, 1929; also Axelrod, 1939).

Chaney (1940*a*) has shown that the isoflors of this period had approximately the same orientation as those of the present, but that they lay approximately 10° of latitude farther north. Several explanations have been offered to account for such climatic differences in time; perhaps the most convincing is that tentatively advanced by Berry (1922, 1930). He suggests that the periods of widest extension of equable and mild climates of the past have coincided with sea extension and the reduction of land areas, and believes that an increase in sea area and a corresponding extension of oceanic climates, combined with a relatively low relief of the continent and free circulation of water into the Arctic, were sufficient to permit the observed shift in isoflors. Such conditions evidently obtained in Eocene time. In Oligocene time, however, land connections were renewed, and not since then have there been as free water connections between the equatorial and arctic regions, nor, apparently, has the relief been as low, at least in the western United States. During the Upper Oligocene and early Miocene, with the re-emergence of land, notably in Eurasia, the closing of the Bering Strait, and the increase in relief, climatic changes toward a cooler and drier climate were initiated which eventually pushed the isoflors southward to their present latitudes.

Evidence that this trend began during the later Eocene and Oligocene is found not only in fossil vegetation, but also in mammalian remains, such as the Sespe fauna (Stock, oral communication; see also Stock, 1936). According to Stock, this fauna, which occurs in a number of localities in Ventura County, California, extends in time from the Upper Eocene to the Lower Miocene. The earlier deposits are correlated with the upper Uinta of Utah, the later ones with the lower Harrison and John Day. The earlier assemblages embrace such forms as the small titanotheres, insectivores, tapir, and small primates similar to the present-day *Tarsius,* and strongly suggest a group of forest dwellers. The ecology of the later assemblages, the chevrotain-like *Hypertragulus* and a camel, is equally suggestive of grazing animals which would

inhabit a savanna. Such forms were followed in mid-Miocene by an influx of well defined grazing types. The paleobotanical evidence for this climatic change has been described by Axelrod (1939). In the eastern United States, the cooling climate is reflected in the floras described by Berry (1916*a, b, c, d;* see also Condit, 1938), and, according to him, the flora of that region had nearly reached its modern status by the Pliocene.

By the end of the Miocene the Arcto-Tertiary forest had seemingly migrated along the central highlands as far south as central Mexico and Guatemala. No fossil evidence supports this assumption as yet, but this seems the only explanation for the presence today in both central Mexico and Guatemala of a mixed temperate forest similar to the Mascall and Florissant floras of the Miocene and Oligocene, particularly in view of the middle and late Tertiary history of the southwestern United States and the geology of Mexico. The nature of this expanding temperate forest is illustrated by the Bridge Creek flora (Chaney, 1924, 1925*a*, 1927), which in Oregon displaced the subtropical Clarno flora. Chaney recognizes in it four elements, (*a*) a West American Element, (*b*) a Southwest American Element, (*c*) an East American Element, and (*d*) an East Asian Element. The outstanding characteristic of the Redwood Component of the West American Element is its resemblance, both in flora and in approximate proportions, to the redwood forest which has now been restricted to the coastal strip of northern California.

That the trend toward greater aridity which began in the Oligocene continued during the Miocene is indicated by the floras of the Middle and Upper Miocene described by La Motte (1936), MacGinitie (1933), and particularly by Chaney (1925*b*; see also Berry, 1929). The Upper Miocene Mascall flora, described by Chaney from central Oregon, was a widespread community of more arid requirements than those of earlier age, and strongly suggests a relationship to the oak-madroño forest found peripheral to the redwood forest of California of today, but it included in addition genera no longer found on the Pacific slope.

The trend toward greater aridity illustrated by these floras was more pronounced in the southwestern United States and in the interior, and in response to it there developed in these areas, displacing the forests of the Eocene, two vegetational types which are new to the historical record: grassland, with a varied and extensive fauna; and a sclerophyll woodland, the Madro-Tertiary Flora, with which the grass was associated in many parts of its area. Grasses are known as early as the Florissant, a temperate border forest of the Oligo-Miocene of Colorado in which savanna was evidently present, and in the plains states grassland as a community was well developed by mid-Miocene. The present-day occurrence of grassland relicts, and the great variety and wide distribution of Miocene and Pliocene grazing animals, suggest that savanna or grassland, or both, extended from the plains states to California, perhaps even in the early Miocene (Elias, 1932, 1935; Merriam and Sinclair, 1907; Clements, 1936; Chaney and Elias, 1936; Stirton, 1936; MacGinitie, 1937*a, b;* Axelrod, 1939; Elias, 1942). The second type of vegetation which was men-

tioned, the sclerophyll woodland, was a generalized arid vegetation of the north Mexican plateau. This woodland had come into existence by the end of the Oligocene (Axelrod, 1939, 1940*a, c*), and, although its extent at that time can only be inferred, it may have occupied much of the southwestern United States by the beginning of the Miocene, inasmuch as elements of it are associated with the Florissant. During Miocene time it too spread widely, replacing the forest, and by the end of the period elements had reached the High Plains, the Columbia Plateau, and southern and central California.

The most extensive of the arid Miocene floras which has been reported upon is the Tehachapi flora (Axelrod, 1939), found near the town of Tehachapi, California. It is early Middle Miocene. This flora was a generalized woodland and savanna with which were associated elements which have since become ecologically segregated in various parts of the former range. The nearest present-day equivalents of this Tertiary woodland are found in southern Arizona and the northern Sierra Madre of Mexico. The climate of Tehachapi time was probably comparable with the climate of that region today, that is, was of a continental type with extremes of temperature and apparently with two rainfall maxima, in winter and in summer, with an inferred range in rainfall of from 12 to 15 inches at lower elevations to 25 inches in the adjacent highlands. With the continued uplift of the western part of North America during the late Miocene and early Pliocene and the consequent development of a rain shadow, elements of this savanna penetrated to central California, to the Columbia Plateau, to central Colorado, and to Oklahoma (Axelrod, 1940*a, b*).

It seems probable, therefore, that during the Miocene the remnants of the subtropical hardwood forest and strand floras disappeared in the West except for coastal relicts, although they have been partially preserved in the extreme southeastern United States, intermixed there with warm-temperate deciduous types. The temperate hardwood forest spread southward over most of the southeastern United States. The temperate mixed forest which had spread as far as Mexico and Guatemala became more and more restricted and differentiated as aridity increased, and its southern elements were ultimately cut off by the spread of a sclerophyll woodland-savanna over a large part of the southwestern states. This arid vegetation reached its greatest extent during the late Miocene and early Pliocene.

During the Middle Pliocene this vegetation, save for relicts, was restricted southward by lower winter temperatures in the Rocky Mountain region and the disappearance of summer rainfall over California and the western Great Basin, and the remaining elements were segregated into the present-day communities, such as the oak-pine woodland, the chaparral, the desert scrub, and the subtropical thorn forest of Sonora. The similarity to the present vegetation of their respective regions of such widely spread Pliocene floras as the Citronelle (Berry, 1916*c*), the Ogallala (Elias, 1932; Chaney and Elias, 1936), the Deschutes (Chaney, 1938*a*), and the Mount Eden (Axelrod, 1937) suggests that the vegetation of North America had assumed essentially its modern

aspect and relative distribution by the end of the Pliocene (see also Axelrod, 1940*b*; Dorf, 1933, 1936), and, according to Chaney (1936*a*), the Pliocene floras of both North America and Asia show a marked resemblance to the modern vegetation of both regions, although there is apparent in most of them a somewhat less arid aspect than exists at present. "The physical conditions characterizing this epoch may be summarized as having involved a topography essentially as diverse as that today, together with a climate in which high range of temperature and annual rainfall varying from 10–12 inches resulted in the development of locally differentiated plant formations with relatively few generic and specific representatives" (Chaney, 1936*a*, p. 78).

Summary

Apart from the tropical biota of Mexico and central America, the biota of western North America has been derived from two sources, namely, a mesophytic temperate biota which was holarctic during the Eocene, and a relatively xerophytic temperate or subtropical biota which developed prior to the Miocene in what is now the north Mexican plateau. The history of temperate western North America since the Eocene is the history of the interactions of these two communities. Both became widespread and, in their earlier stages, were seemingly more generalized in the sense that species were then associated which have since become restricted to more depleted and specialized communities, now geographically and ecologically segregated. This differentiation and segregation is interpreted as a response to a continued trend toward a cooler and drier climate and a more pronounced physiographic differentiation which began during the Oligocene. During the Miocene, or perhaps even earlier, the temperate biota apparently penetrated along the highlands as far as central Mexico and Guatemala, but during or prior to this time it was disjoined from the related biota of the Pacific slope by the development in the intervening area of the xerophytic north Mexican biota. Its reliets are found today in the Pacific Mountain System, the Rocky Mountain System, and the highlands of central Mexico and Guatemala. The north Mexican biota reached its greatest extent in area during the late Miocene or early Pliocene. During and since Pliocene time, it has been somewhat restricted and at the same time segregated into the present communities of the southwestern United States and northern Mexico, but has not been disjoined.

CONCLUSIONS

We have already called attention to the fact (p. 150) that the Santa Cruz arrangement does not in all probability occur in association with the present-day elements derived from the Madro-Tertiary vegetation which now occupy the region between its two areas of distribution. We have also shown that the historical records suggest that this vegetation existed there during the Pleistocene and Pliocene and probably during the later part of the Miocene, if not earlier. Hence, the inference is justified that the populations which carry

this arrangement reached the limits indicated somewhen during the Miocene or earlier and have been disjoined since that time. Support of this view is found in the geological history of the Isthmus of Tehuantepec, which separates the now disjunct populations of the highlands of central Mexico and of Guatemala (and doubtless also Chiapas, which has not been explored for *Drosophila*).

This isthmus is an area of low rounded hills less than 800 feet above sea level, covered with a tropical lowland vegetation. It is bounded by the highlands of Oaxaca on the one hand, and the highlands of Chiapas and Guatemala on the other, and lies between them "like a great block dropped out of an arch." It interposes a climatic barrier which, it would seem, is completely impervious to the migration of *D. pseudoobscura,* barring aerial transport. The history of the isthmus during and prior to the Pleistocene is inferred both from the geology of the region and from the distribution in the Colorado Desert of fossil Caribbean mollusks (see Schuchert, 1935; Woodring, 1932; Olson and McGrew, 1941). From this evidence it appears that the isthmus has been an area of low relief since the Middle or Lower Miocene. During a part of this time, perhaps during part of both the Miocene and the Pliocene, the land was submerged, forming the Tehuantepec portal between the Gulf of Mexico and the Pacific. In the late Pliocene and Pleistocene the isthmus was raised above the sea. There is no evidence to suggest that this elevation was very much greater than at present, and, judged on the basis of the specific differences between the temperate forests of Oaxaca and Guatemala, it was seemingly insufficient to permit a free migration of the temperate biota between these regions.

If these conclusions are sustained it appears that Santa Cruz has been in existence over much of the present specific area since the Miocene, or even earlier. It will be recalled that this arrangement may be the initial one of the whole phylogeny. Today, the populations which carry it are restricted to mild and equable climates and are associated in each of the disjunct areas with the least modified of the Arcto-Tertiary Flora. It is perhaps more than a striking coincidence that Standard, which may also be the initial arrangement, is centered in California under the same conditions. Furthermore, a majority of the arrangements occur today largely in association with the present-day derivatives of the Arcto-Tertiary Flora. It is, therefore, reasonable to suppose that the species itself has been chiefly a part of that biota throughout the period indicated, and has been subject to its vicissitudes.

Support of this conclusion is found in the present distribution of other members of the species group to which it belongs, the *obscura* group of the subgenus *Sophophora* (Sturtevant, 1942). This group is formed of two alliances, to one of which are referred *D. pseudoobscura, D. persimilis,* and *D. miranda,* all inhabitants of western North America, and *D. obscura, D. subobscura,* and *D. tristis,* together with several undescribed species, all of which are found in Europe. Whether the group occurs also in eastern Eurasia is unknown for want of exploration, but it would not be surprising to find it in the highlands

of southeastern China, or in eastern Siberia, in view of other distributions. This alliance is close-knit, with relatively slight morphological differentiation (see part I). The European species are known chiefly as laboratory animals, but, to judge from the regions whence they have been described, are also associated with European relicts of the Arcto-Tertiary Flora. No interchange of this biota with that of North America is known to have taken place since early Tertiary time. Hence the species group as a whole is very ancient and holarctic.

The question can justly be raised whether this species group of *Drosophila* is unique in its present-day distribution. Do any other phylads extend from Europe to Guatemala? Do any other phylads occupy only the disjunct areas which the arrangements of *D. pseudoobscura* occupy? Do any other phylads suggest an infiltration between these disjunct areas? To all these questions a positive answer can be returned.

The occurrence in both North America and Eurasia of plant or animal species or species groups is not uncommon, and some which are found on both continents have distributions which parallel the distribution of the present-day remnants of the Arcto-Tertiary forest. Of these, *Chimaphila umbellata*, a well marked species of the heather family, can be cited as an example. This species occurs in northern Europe in the same regions as *D. obscura* and *subobscura*, and again in Japan. In somewhat different form (var. *occidentalis*) it is a familiar plant in the temperate forest of North America southward to southern California, to northern New Mexico, and to northern Georgia. It reappears again in the temperate forest of central Mexico, from Vera Cruz to Oaxaca, and again in Guatemala. It is generally agreed by systematists that distributions of this kind imply a holarctic dispersal.

The distribution of *Mahonia fascicularis-pinnata,* a species or species group of barberry, parallels in a remarkable way the distribution of the Santa Cruz arrangement. This group, which is considered by Standley (1922) to be conspecific, is found in coastal California from the Bay region southward to San Diego County and on Santa Rosa and Santa Cruz islands. In Mexico, like *Chimaphila umbellata,* it ranges from Vera Cruz to Oaxaca, and it reappears in the highlands of Guatemala. These are almost precisely the areas to which Santa Cruz is restricted so far as we know at present.

It will be recalled that the arid region which intervenes between the concentration of the Santa Cruz phylad in California and that in central Mexico is occupied principally by Chiricahua, which is thought to be the dominant arrangement there. If we assume that Santa Cruz was an occupant of the Tertiary forest prior to its restriction, then it would follow that Chiricahua has since occupied the intervening territory in association with the Madro-Tertiary Flora. What appears to be a parallel example in the closely knit and distinctive phylad *Cupressus* has been kindly brought to the writer's attention by Carl B. Wolf, the student of this genus. In North America *Cupressus* is found only in California, in Central Mexico and Guatemala, and in the intervening region. In California a number of species are found, in which Wolf

discerns four species groups. Of these, one group is restricted to a narrow range along the coast of California in Monterey, Santa Cruz, and Mendocino counties. Of the four species, three are extreme endemics, two being restricted to the Monterey Peninsula and one to the Santa Cruz Mountains; the fourth is more widespread along the coast of Mendocino County. The closest alliance of this phylad is not with the remaining species in California, but with a species or species group of central Mexico and Guatemala (the specific limits and range of this group are as yet uncertain). Between these two alliances, thus restricted in distribution, is a third of several widespread species typified by *C. arizonica,* which range from the interior of California and the North Coast Ranges southeastward through the mountains of Arizona and New Mexico to central Mexico. In other words, the relative distribution of these *Cupressus* species groups closely parallels that of Santa Cruz and Chiricahua. (It is of interest to note that Axelrod, 1939, has referred the Miocene cypress of the Tehachapi flora, *C. mohavensis,* to relationship with *C. arizonica,* partly on ecological grounds, it is true.)

If we may accept the evidence presented above for the disjunction of the Santa Cruz phylad and at the same time believe that aerial transport has not been a factor in producing the pattern of its distribution, then it follows that not only Santa Cruz, but also its derivatives of the second and third degree, Tree Line, Cuernavaca, Olympic, and Oaxaca, were in existence during Miocene time or perhaps earlier. We advance this as an hypothesis and from it suggest a tentative history of the species. This hypothesis and history may be very far from the truth. It is possible, as originally implied by Dobzhansky and Sturtevant (1938), that the present distribution of gene arrangements took place in relatively recent time, perhaps Pleistocene or post-Pleistocene. Nevertheless, the facts we have presented in parts I and II seem to require another explanation. If the phenomena described are not a product of Pleistocene movements of biota, then they are seemingly best explained by our hypothesis. The suggested history is as follows:

The progenitor of the *obscura* species group was a member of the Arcto-Tertiary temperate forest. Spreading with this forest, it differentiated into the present species, which became restricted to the Eurasian or North American elements of the forest. The species restricted to North America were *Drosophila pseudoobscura* and *D. miranda,* which may or may not have been specifically segregated at that time. It will be recalled that we have mentioned the arrangement "Hypothetical" with the observation that, although its existence has been predicated, the arrangement has not as yet been found. This arrangement is of especial interest because it closely resembles the gene arrangement of the third chromosome of *D. miranda.* Hence, there is good reason to consider it the probable initial arrangement, a conclusion which is also supported by its central position in the phylogeny. In any case, it is possible that Standard, Hypothetical, and Santa Cruz were all present in the Arcto-Tertiary forest. Tree Line and its derivative Olympic must also have been in existence before the forest was disjoined, and Cuernavaca and Oaxaca before the dis-

junction of the Mexican and Guatemalan populations. We have no means of fixing the relative time of appearance of the remaining arrangements, but it is a fair .assumption that the secondary or tertiary derivatives which are known from only a single limited area were formed later. Nor can we fix on any time for the origin of the arrangements of *D. persimilis*. If, however, we may believe that Olympic and Oaxaca, both tertiary derivatives, were in existence during the Miocene, it is reasonable to suppose that other arrangements of secondary order may have been also, including those of *D. persimilis*.

Santa Cruz, Tree Line, and Olympic may all have been formed in a population adapted to the relatively uniform and equable conditions of the Arcto-Tertiary forest, and spread with it widely. Being more limited in tolerance, this population has survived chiefly in the forests of central Mexico and Guatemala, which in many respects resemble the generalized forest from which they were derived more closely than present-day remnants of the Pacific slope. After this forest reached central Mexico and Guatemala, Cuernavaca and Oaxaca may have been formed. With the beginning of the restriction and segregation of the forest, Estes Park and Chiricahua may have been formed in association with some gene or gene frequencies which enabled the population to expand into the developing communities which it now occupies, the latter becoming adapted to elements of the Madro-Tertiary Flora and spreading with it into the Great Basin. The low concentration of Chiricahua in east central Mexico and in the Rocky Mountains and its absence from Texas and west central Mexico suggest a possible spread from a forest such as the Mascall. Estes Park may have originated in some phase of the Florissant and spread southward. Hidalgo, Mammoth, and San Jacinto may be comparatively recent arrangements which are still confined to their places of origin.

Standard may have been formed in a population adapted to a border forest such as the Mascall, and has survived in the forests of the Pacific slope which were derived from that community. Arrowhead and Pikes Peak, like Chiricahua, may have been formed in peripheral populations of the Mascall or Florissant and expanded into the Madro-Tertiary woodland, then spreading northward from Mexico. Texas and Cochise may represent relatively recent arrangements.

The occurrence of the Standard arrangement in both *D. pseudoobscura* and *D. persimilis* suggests that the latter may have originated in a community similar to the Mascall and since remained associated with its derivatives along the Pacific coast, where the other arrangements of this phylad were subsequently derived. It occurs in areas which are dominated in *D. pseudoobscura* by Standard and Arrowhead. There is the possibility, of course, that the Standard arrangement of *D. persimilis* is the initial form. Yet this seems improbable in view of other distributions.

Little can be said of *D. miranda,* the limits of which are more or less coextensive with those of *D. persimilis,* but which is infrequently found. The fact that the gene arrangement of its third chromosome closely resembles the expected Hypothetical arrangement of *D. pseudoobscura* suggests that it is con-

temporary with the latter or older. Its occurrence in California suggests that it has had essentially the same history.

A fourth species, *D. azteca,* is known to occupy an area similar to that of *D. pseudoobscura,* and included by it, but less extensive. It also is a member of the *obscura* group, but forms an alliance with *D. affinis, D. athabasca,* and others (Sturtevant, 1942), which occupy most of North America exclusive of the territory occupied by *D. pseudoobscura.* It is centered chiefly in central Mexico and Guatemala, but ranges northward to the Huachuca, Chiricahua, and Santa Rita mountains of Arizona, the Pinos Altos and Mogollon mountains of New Mexico, and the Chisos and Davis mountains of Texas. It also occupies a widely disjunct area in northern California. If present in the intervening territory, the species is assuredly rare. In view of its parallel distribution, the distribution of its gene arrangements is of added interest. The data available are by no means so extensive as those for *D. pseudoobscura,* but nevertheless are sufficient to be indicative.

Inversions have been studied in the long limb of the X chromosome, in the proximal and distal parts of the B chromosome, and in the A chromosome (Dobzhansky and Socolov, 1939; Dobzhansky, 1940). Their distribution presents much the same pattern as does that of the gene arrangements in *D. pseudoobscura,* and suggests a spread from north to south (or vice versa), during the course of which the inversions occurred more or less successively. The direction of the phylogenies could not be ascertained as in *D. pseudoobscura,* but none of the distributions is incompatible with the conclusion that the history of this species is essentially the same. If so, the Beta arrangement of the X chromosome, the Beta arrangement of the proximal part of the B chromosome, and the Delta arrangement of the distal part would all presumably be initial, inasmuch as these and only these occur both in California and in central Mexico. The arrangements of the C chromosome are not so clear. Alpha, Beta, Gamma, and Delta parallel the distribution of Santa Cruz in Mexico and Guatemala. Epsilon, Zeta, and Eta recall that of Standard. But it would not be surprising to find either Alpha or Beta in California, in which case the distribution of the gene arrangements in *D. azteca* would parallel that for *D. pseudoobscura.*

In view of the extraordinary evolutionary activity among grazing animals which took place during the Tertiary, it may seem remarkable that the species of *Drosophila* should have remained comparatively static, if indeed they did. It should be remembered, however, that the mammalian fauna, both carnivorous and herbivorous, so richly represented in the Miocene and Pliocene arose in response to the widespread development in North America and Eurasia of a novel vegetational type, the temperate grassland, unparalleled as a reservoir of available foodstuffs. *Drosophila,* on the contrary, is primarily a forest dweller, and an inhabitant of the Tertiary temperate forest. During much of the Tertiary and down to the present day the history of this forest has been one of continued restriction, decimation, and fragmentation, rather than migration and expansion, such that the typical genus *Sequoia,* which prob-

ably ranged as widely during the Eocene as the grazing animals ranged during the Pliocene, is now on the verge of extinction. Cockerell (1917), in reviewing the progression of fossil insects, has noted a similar contraction, since the Oligocene, of the insect fauna which is so richly represented in the Florissant shales and the Prussian amber. With these in mind, he speaks (p. 9) of the Tertiary insect fauna as "essentially modern, indeed it may be said that we have it still with us," and (p. 11) quotes Wheeler, referring to the ants of the Oligocene amber: "The family has not only failed to exhibit any considerable taxonomic or ethnological progress, but has instead suffered a great decline in number of species and therefore also in the variety of its instincts, at least in Europe." There is fossil evidence, therefore, which suggests the development of an essentially modern insect fauna with the spread of the Arcto-Tertiary forest.

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